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Between Conflict and Cooperation: New Horizons in the Evolutionary Science of the Human Family

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Abstract

Familial relationships cannot be properly understood outside of an evolutionary framework. Pseudoscientific and traditional modes of thought have steered us away from an accurate account of ourselves and our kin. Recent theoretical and empirical advancements in the evolutionary sciences, such as the theories of inclusive fitness, parental investment, and parent-offspring conflict, have aided our understanding of familial conflict and cooperation. We suggest that a gene's eye perspective of human families can likewise illuminate much of human psychology and behavior by contrasting individual interests with genetic interests. Furthermore, genetic imprinting and extended phenotypic action-at-a-distance have unveiled the extent to which coevolutionary arms races and manipulation may lie at the heart of familial interactions and psychological disorders. We posit that human cultural trends and morals can ultimately be grounded on an evolutionary foundation: not only do human laws and institutions reflect group-level manifestations of gene-level cooperative adaptations, they may also reflect gene-level manipulative adaptations. An awareness of evolutionary dynamics can advance human well-being and unveil the hidden mechanisms beneath all human and non-human relationships.

Keywords: family relationships; kin selection; inclusive fitness; evolutionary psychology; extended phenotype; cooperation; conflict; adaptation

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Introduction

For all the time that we spend with and think about our kin, accurate information on the workings of the human family is hard to come by. Amid the current of popular talk shows like Dr. Phil or Dr. Laura, as well as a host of books and self-help phenomena, there is little honest, reality-based information to help us understand our familial relationships. There is, however, much proselytizing by religious figures and media ideologues on the breakdown of the modern family. Self-titled gurus and even some medically trained professionals are disseminating advice that is false and sometimes dangerous. Although this volume is not meant to offer therapeutic guidance for mending the wounds of familial conflict, it does provide an empirically tested account of the dynamics behind family relationships. By understanding our evolutionary past and the selection pressures that bombarded our ancestors, we can begin to form a stable foundation that will guide our academic, practical, and ethical decisions in dealing with the trials and tribulations of kinship.

The Unveiling of Familial Nature

Just as Rousseau's (1755) depiction of a wholly peaceful human nature was overturned by Darwin's (1859) theory of natural selection, current explorations in evolutionary biology and psychology cast doubt on the idea that a family is a coherent unit of cooperative individuals, with familial conflict only occurring when otherwise functional family relationships break down. With the modern evolutionary synthesis in biology, as well as the subsequent developments of kin selection and selfish gene theory, science has been unveiling the extent to which familial conflict is the product of selection. William Hamilton's (1964) theory of inclusive fitness provided a theoretical framework for predicting instances of familial discord as well as cooperation. According to this theory, the more genetically distant a relative is from another relative, the more likely it is that conflict between them will occur. In fact,

when there is any genetic heterogeneity between interacting individuals, some form of conflict between them is inevitable, regardless of whether they are related. Distant relatives do not share as many genes for helping one another as do close relatives. For example, because monozygotic twins share 100% of their genes, they are likely to reproductively value each other as much as they value themselves. Meanwhile, parent-child and full sibling relationships, which are based on a genetic similarity of only 50%, are expected to exhibit conflict as well as cooperation. The same reasoning can be extended to more distant networks of interrelatedness, with individuals investing more in their grandchildren, for instance, than in their third cousins (see Euler, Ch. 12, this volume). Of course, the proportion of shared genes is not the only factor determining how much investment is provisioned to family members. Ecological circumstances such as the availability of food, as well as the health, age, and reproductive prospects of family members are also considerations that are taken into account when deciding whether to benefit one's kin (see Del Guidice & Belsky, Ch. 5, this volume, for life history tradeoffs in parental care).

In general, organisms tend to behave indifferently toward one another. Outright cooperation and conflict are costly and are only engaged in if the reproductive benefits outweigh the expenditures in time and energy. In many species, even relatives tend to be ignorant of each other's existence. In some species, however, genes that code for altruism toward kin may spread within a gene pool by favoring relatives who are likely to carry copies of the same genes. Such is the case with humans. Our nepotistic tendency is a result of millions of years of selection for genes that selfishly benefited copies of themselves. While our proximate thoughts and feelings enable us to feel love and affection for our family members, the ultimate evolutionary reason behind that love and affection is genetic self interest—although of course this in no way invalidates the power and importance of such feelings. Furthermore, when there is genetic incongruity between kin that spend a great deal of evolutionary time interacting with one another (as parents and children do within our own species, which is characterized by a prolonged period of dependence on parental care; see Periss & Bjorklund, Ch. 10, this volume), coevolutionary arms races are expected to occur. Far from being confined to predator-prey interactions,

arms races characterize many of our most cherished familial relationships. The human family is rife with evolved weaponry for mutual exploitation.

All's Fair in Love and War

Following in Hamilton's footsteps, subsequent investigations in the biological sciences brought us face to face with the realization that familial conflict runs deeper than expected. In a series of groundbreaking papers, Robert Trivers examined a number of adaptations that organisms possess for manipulating and extracting resources from their kin. His theory of parental investment (1972), for instance, examined the diverging reproductive interests of males and females. According to parental investment theory, the sex with the greater minimum obligatory investment necessary to produce and rear offspring to reproductive age will be the more discriminating sex when it comes to choosing sexual partners. In most mammals, females incur greater minimum reproductive costs than males as a result of pregnancy and lactation. By choosing the wrong male, females risk jeopardizing their valuable reproductive resources by investing in genetically inferior offspring or risk copulating with a male who is unlikely to provide the resources needed to help her successfully raise an offspring to adulthood. As a result, females are expected to have evolved psychological adaptations for discriminating genetically superior and resource-rich suitors from genetically inferior and resource-deficient suitors. In contrast, males are likely to have evolved their own adaptations for attempting to copulate with as many females as they can (since males pay less in reproductive costs when copulating with genetically inferior females than vice versa) and for minimizing investment in offspring that they did not sire. This war of the sexes has been raging as a coevolutionary arms race between ancestral males and ancestral females. Although sexual reproduction can be a cooperative venture by which males and females replicate their genes, we must all come to terms with the possibility that human romantic relationships are rife with deceptive and manipulative strategies that were selected into each sex because they proved successful at manipulating members of the opposite sex.

In humans, women may manipulate men to extract resources (by promising them sexual favors, for example), prevent them from investing in rival women and their offspring through psychological manipulation and commitment jealousy, or cuckold them by surreptitiously producing offspring sired by genetically superior men (see Buss, 2003, for review). Men, on the other hand, are more likely to deceive women into thinking that they are of higher genetic quality or are better able and more likely to invest in long-term romantic commitment and childrearing than they actually are. Along with body language and verbal behaviors, members of both sexes may use clothing, makeup, and accessories to manipulate members of the opposite sex as part of their reproductive strategy. Manipulative reproductive strategies vary by sex (see Buss, 2003, for review): Women are more likely to engage in appearance enhancing behaviors to communicate youth and fertility, and men are more likely to exaggerate their wealth, generosity, and social standing to communicate their willingness and ability to invest in a woman and her offspring. Men also possess a host of adaptations for manipulating the sexual behavior of their partners to minimize the risk of investing in offspring sired by a rival (see Goetz & Romero, Ch. 11, this volume). These adaptations include abusive and intimidating tactics as well as generous and affectionate behaviors aimed at preventing female infidelity (Miner & Shackelford, 2010). Male and female sexual strategies, however, do not all fit the same pattern and may vary across an individual's lifespan as a result of contextual and life history circumstances, although genetic differences can account for the influence of personality characteristics on sexual strategies (see Kaighobadi et al., 2009, for the effect of male personality traits on the risk of partner-directed violence). Sexual jealousy as an evolved response to ancestral selection pressures of paternity uncertainty and the risk of partner abandonment may thus shed light on such divergent behaviors as romantic affection and spousal abuse.

On average, men are more interested in sexual variety than women. Some men, however, may eschew a polygynous strategy in favor of a long-term commitment to a single woman, provided that such a strategy was reproductively successful for their male ancestors. The evolution of long-term pair bonding mechanisms within men and women may have brought about selection for the intensely felt and

overpowering emotional reactions that characterize romantic love (see Buss, 1987, 2003). Such a seemingly irrational commitment to a member of the opposite sex may have been adaptive for our ancestors in motivating them to remain together to raise an altricial child. Future investigations into male-female interactions are needed to further map the structure and function of the adaptations employed by each sex against the opposite sex in the mating arena. The application of sexual selection theory (Miller, 2000) to human mating strategies may likewise illuminate our understanding of human culture as a tool that is used to attract mates by communicating one's genetic worth or resourcefulness. Evolutionary approaches to human psychology and behavior can thus provide valuable insights into the origins and functions of our most sublime passions and affections.

Parents and Children

Our conception of the parent-offspring relationship as the paragon of familial harmony is likewise being overturned by current investigations into parent-offspring conflict. The bond between a mother and her child is often regarded as the most pure and sacred of all family relationships. This sentiment is expressed in the iconic Christian image of Mary cradling her infant, a depiction of unbridled love and nurturance. Such idyllic cultural imagery, however, belies a more nuanced biological reality. Although the mother-child relationship is largely based on the evolutionary necessity for care and protection of altricial infants and children (see Periss & Bjorklund, Ch. 10, this volume), and although there are countless examples of parents sacrificing their own lives on behalf of their children, Trivers's (1974) theory of parent-offspring conflict posits the existence of an arms race between the reproductive interests of parents and offspring that may even lead to instances of child abuse and filicide. The evolutionary reason for this conflict boils down to sibling rivalry. Disregarding factors such as offspring age and health, a diploid mother's genetic interests are usually best served by apportioning her resources equally among all her offspring because that mother shares the same proportion of her genes with each of them (50%). Each offspring, however, values its own genes over the genes of its mother and siblings, and although relatives are more likely to cooperate than nonrelatives, the genetic interests of the offspring are

sometimes best served by extracting more resources from its mother than the mother is willing to allocate. This resource extraction comes at the cost of the reproductive success of the offspring's mother and its current or future siblings, leading to the evolution of adaptations for manipulation on the part of both parents and offspring. In certain contexts, therefore, the genetic interests of parents and offspring are at cross purposes (see Salmon & Malcolm, Ch. 6, this volume). Even though we are one of a few mammalian species in which fathers also provide a certain amount of childcare, mothers are still the primary caregivers in almost every society. As a result of these selection pressures, parent-offspring conflict is mostly fought between mothers and offspring (but see Del Guidice & Belsky, Ch. 5, this volume, for cases in which paternal and maternal genes compete within a single organism via genetic imprinting).

The tug-of-war between a mother and her offspring is evident at conception. Although the uterus is usually an ideal environment for a developing fetus, a fetus's adaptations for extracting nutrients from its mother may sometimes trigger the mother's physiological adaptations for limiting resource allocation to the fetus. In such instances, a fetus is considered to be parasitic on the mother and may even bring about a miscarriage. For an expectant mother, a miscarriage can be an earth-shattering experience. From an evolutionary perspective, however, it may reflect an adaptive response on the part of the mother's body that may ultimately save her life. This may have been a last line of defense for an ancestral mother whose Pleistocene environment lacked the amenities of modern medicine.

If the infant survives gestation, its struggle with its mother over nutrients and maternal affection takes on wider behavioral dimensions. Infant crying, for instance, may signal an infant's genuine need for protection or sustenance, or be used as an honest indicator of infant fitness, but it can also be manipulatively employed by the infant to prevent mothers from copulating and giving birth to sibling competitors (e.g., Lummaa et. al. 1997). For the same reason, a child may delay its time of weaning for the sake of limiting resource diversion to its current or future siblings. As children mature, sibling rivalry and parent-offspring conflict may be expressed in the contexts of playground privileges, priorities to the

biggest portion of dessert, or demands for the best Christmas present. Once puberty arrives, adolescents and parents may engage in conflict over adolescent mating decisions (Apostolou, 2009). For example, parental genetic interests may be better served by their daughters engaging in long-term mating, but daughters may reproductively benefit their own genes by engaging in short-term mating and relying on parents to help them raise resultant offspring. Thus, parent-offspring conflict may be in motion whenever parents prevent adolescents from associating with members of the opposite sex of whom they disapprove. Likewise, adolescents can adaptively rebel against their parents' wishes by staying out late or keeping friends whose influence upon their sexual behavior may conflict with parental interests. The hidden biological dynamics of parent-offspring conflict over mating decisions may yet explain the timeless appeal of Shakespeare's *Romeo and Juliet*.

All evolutionary relationships fall along the continuum of conflict at one end and cooperation at the other. Relationships between different genes and organisms reflect the selection pressures that gave rise to them. Some of these relationships are characterized by mutual benefit, while others reflect generations of continuous conflict and arms races. Evolutionary relationships characterized by genetic kinship, however, fall somewhere in between the two extremes. Although an organism may reap genetic benefits by investing in kin with whom genes for benefitting kin are shared, exploitation of one's kin is also to be expected when there is genetic distance between the interacting kin. Furthermore, adaptations for dealing with kin may be extended or co-opted when genetically unrelated organisms benefit from or parasitize one another via the redirection of adaptations that are normally aimed at benefitting or manipulating relatives (see Archer, Ch. 16, Serpell & Paul, Ch. 17, Qirko, Ch. 18, and Ackerman & Park, Ch. 19, this volume).

The Long Reach of Our Genes

We are fractionated from within and without. No longer can we consider ourselves to be working solely for the evolutionary benefit of our individual selves. Hamilton's (1964) theory of inclusive fitness

and Dawkins's (1976) popularization of selfish genes brought about the realization that genetic interests do not always coincide with the interests of the individual organism. It may be helpful to view the family as consisting of networks of genes that seek to propagate themselves by coding for programs that either benefit and form alliances with one another, or exploit one another, rather than as consisting of individual family members. The evolutionary success of these programs is ultimately judged by whether the genes coding for them are naturally selected over rival alleles within the gene pool. To the extent that a novel mutation contributes to the cooperative or manipulative effort of programs that function within the family environment, it will propagate itself within the gene pool and contribute to the coevolutionary processes that characterize kinship relations. Indeed, this perspective helps to illuminate the evolution of all biological systems.

The relationship between a gene and its phenotypic effect(s) is non-linear. The developmental process is characterized by a complex bi-directionality whereby a gene's expression is dependent upon the other genes within its environment as well as upon the ecological cues that activate it (see, for review, Bjorklund & Pellegrini, 2002). This leaves much room for the influence of competing genes upon the development of a gene's phenotypic expression, whether anatomical, physiological, psychological, or behavioral. To the extent that we spend a substantial portion of our lives surrounded by kin, beginning with conception, there is much opportunity for our close kin to manipulate the developmental outcomes of our phenotypic programs. Our genes, however, are not idle pacifists and do not absorb without recourse the manipulation of their developmental expression; our ongoing evolution has likely brought about the selection for phenotypic defenses against the manipulative nature of certain genes possessed by our kin. This may have resulted in an arms race whereby our kin's genes are selected for how well they can direct our ontogenetic course for their own benefit, and our own genes are selected based on the criteria of how well they can code for phenotypic expressions that resist being manipulated during our development (which may help to explain the paradoxical finding that parental rearing practices have little direct effect on subsequent offspring outcomes, although it remains to be seen whether parents may influence their

offspring's development via more implicitly acting adaptations to parent-offspring conflict; see Harris, 2009). This genetic battle can even occur between the maternal and paternal genes within an individual organism, whereby one parent's genes can code for physiological processes or behaviors that inflict a cost upon the genes of the other parent (see Del Guidice & Belsky, Ch. 5, this volume). In this sense, it is more accurate, biologically speaking, to view families as self-promoting networks of genes rather than as self-promoting individual organisms.

We likewise possess the same adaptations for manipulating as well as benefitting our own offspring, provided that we ourselves reproduce. Thus when we are in the role of offspring, certain genetic programs and psychological mechanisms for extracting resources from our caregivers are turned on, while other, contextually irrelevant programs and mechanisms are turned off. Once we become parents, latent genetic programs and psychological mechanisms for manipulating as well as benefitting our own offspring come online. In a spectacle of evolutionary irony, the inherited evolved programs and mechanisms used by our parents to manipulate us in our youth are used by us as tools to manipulate our own offspring. Such is the evolutionarily derived cycle that characterizes our developmental journey through life.

According to Del Guidice and Belsky (Ch. 5, this volume), parental investment strategies can influence offspring attachment styles, pubertal timing, and sexual behavior. Girls that form insecure attachments to their fathers, for instance, are more likely to experience an earlier onset of menarche and pregnancy than do girls who receive reliable paternal resources and care. This parallels Maestripieri et al.'s (2009) work showing how maternal styles can influence the subsequent developmental trajectories of rhesus macaques. These findings may be interpreted by positing that parents have evolved manipulative strategies to influence the physiological, psychological, and behavioral development of their children. On the opposite side of the arms race, children may have evolved defensive strategies to minimize the influence of parental strategies on their development. It may be that children's developmental outcomes are not only the results of parental manipulation but also reflect evolved solutions to the life history trade-

offs that they experience throughout their development. Both scenarios should be investigated empirically.

Whenever one organism manipulates the behavior of a different organism (more specifically, whenever a gene manipulates the action of a different gene) for its own reproductive benefit, it is using the manipulated organism (or gene) as an extended phenotype of itself (Dawkins, 1982). This action-at-a-distance gives manipulator programs long-reaching power in manipulating their environments. The manipulated organisms can be viewed as phenotypic manifestations of manipulator organisms. This approach can help us to understand intersexual and intrasexual relationships, as well as parent-offspring relationships. Coevolutionary relationships between members of the same species may result in selection for mutually manipulative strategies that are either evolutionarily stable, in which each strategy is at its adaptive peak and can do no better, or evolutionarily unstable, in which a runaway arms race ensues and ever-more manipulative, counter-manipulative, and defensive strategies evolve. Both stable and unstable arms races are probably present in our own species, in which individuals have evolved strategies to use other individuals as extended phenotypic tools for their own benefit (see, for review, Dawkins, 1982).

Humans may manipulate each other in circumstances in which deception and manipulation helped our ancestors best their reproductive rivals by controlling the rivals' behaviors. Studies of language use within politics, economics, and everyday situations can aid our understanding of how our evolved predispositions for deceiving our rivals are verbally and culturally expressed, and how language and culture may in turn influence the evolutionary and developmental trajectories of our manipulative extended phenotypic adaptations. Likewise, the proximate manifestations of parent-offspring conflict can be examined from the perspective of the extended phenotype by measuring individuals' behaviors as a function of their kin's manipulative strategies. For example, young mothers with high future reproductive prospects may seek to limit their investment in reproductively unsuccessful offspring by manipulating their offspring's psychological state or behavior. In a study by Brown et al. (2009), university students' risk of suicide was predicted by their mother's age, how burdensome they felt they were to their families,

and their degree of romantic satisfaction. Therefore, parents may possess adaptations for relieving their burden of a reproductively unsuccessful child by using that child as an extended phenotypic tool of their own reproductive interests. Thus, parental adaptations for manipulating offspring psychology and behavior may have been selected into our gene pool if these adaptations successfully brought about the death of a reproductively unpromising and resource-draining offspring. Parental manipulation of offspring depression and suicidal ideation may have had lower social costs than direct filicide and thus, along with filicide, may have been selected into our gene pool. Suicide may even prove adaptive to the offspring's own genetic interests provided that the genes coding for kin-directed altruism are benefitted thereby. Likewise, parents may use their children as extended phenotypic tools to acquire sexual partners, similar to the way in which individuals may use their pets to show off their resources or empathetic qualities to potential mates (see Serpell & Paul, Ch. 17, this volume). In the future, researchers might investigate the specific behavioral, neural, and hormonal pathways by which individuals influence the emotions, cognitions, and behaviors of other individuals. Of course, such a scientific investigation in no way excuses psychological abuse, filicide, or the manipulation of individuals; understanding the evolved strategies that humans employ against other humans does not morally sanction them.

The cultural correlates of parent-offspring conflict can be analyzed by examining the extent to which parents, offspring, and siblings use tools and technologies to influence each other's behavior. The telephone and internet may be useful tools for manipulating our families, friends, and neighbors. Parents may retain some extended phenotypic power over their children (regardless of whether their children are in the same household) if they continue to influence their children's behavior. For example, cellular phones and computers may provide parents with effective means of manipulating their physically distant children's reproductive behaviors by sending their offspring dating advice through email or text messages. Likewise, children may acquire a larger extended phenotypic reach over their parents if they are technologically savvier than their parents and can use technology to extract resources from them. It is likely that the rapid increase in technological advancement that exemplifies our species has created novel

selection pressures for unpredictable and innumerable runaway arms races between related and unrelated individuals. With the aid of modern technology, our manipulative and defensive psychological mechanisms have acquired unprecedented phenotypic powers.

Therapeutic Implications of the Extended Phenotype

In applying the extended phenotype model to therapeutic settings, we can automatically see the pitfalls of psychologically treating individuals in isolation from their families and social networks. Psychological conditions such as depression and bipolar disorder may in fact be indicative of genetic conflicts between patients and their kin, or internal conflicts between a patient's maternal and paternal genes. If individuals manipulate each other's psychological states and behaviors with evolved manipulative tactics, it is no longer enough to focus therapeutic treatments on individual patients—clinicians must be attentive to signs of psychological manipulation of patients by their families, friends, social structures and institutions, or by some of their own selfish genetic elements. Psychological symptoms such as paranoia may result from hyperactive adaptations that normally protect individuals from being manipulated by other individuals in their environments. Although the government may not be spying on a schizophrenic patient's every move, his or her paranoia may hint at a deeper conflict between the interests of state institutions and the patient's own reproductive interests.

Hearing voices or feeling conflicting emotions and cognitions may result from genetic imprinting of parental genes. Paternal genes may code for psychological systems that conflict with an individual's maternally coded psychological systems, and vice versa. The symptomatic results of this mismatch of psychological processes could be shame, guilt, or suicidal behavior. Patients may feel torn from within and therapists may see no hope for recovery. While medications can greatly reduce some of the worst symptoms of psychosis, and cognitive and behavioral treatments can give patients tools for managing their intrusive thoughts and behaviors, clinicians might devise novel methods for dealing with the reverberations of this internal genetic conflict. Medications for selectively suppressing the action of

genes implicated in genetic imprinting may do well in conjunction with appropriate therapeutic techniques for lessening the burdens of patients.

Likewise, psychiatrists and psychologists might investigate the social and familial frameworks within which their patients operate. Interpersonal and family therapy, combined with evolutionary psychological approaches, can provide important insights for guiding future research into psychological treatments. More specifically, therapists may view the distressing symptoms of patients as effects of manipulative tactics of other individuals. By doing so, therapists can focus their treatments on lessening the burdens of such manipulative tactics instead of treating symptoms as breakdowns in the normal functioning of individuals.

Many of our adaptations for manipulating and deceiving others have been naturally selected to target family members. The reason for this is that most of our ancestors' social interactions were limited to repeated encounters with kin. Thus, there may have been an implicit evolutionary rationale behind the psychoanalytic focus on maternal relationships within the therapeutic setting. Freud's folly, however, was in positing familial dynamics for which there was, and still is, little empirical support. The dynamics behind parent-offspring conflict, however, have been documented in a number of widely diverse species, including humans. Post-partum depression, for example, may represent an evolved response on the part of a young mother to a resource-draining infant (e.g., Hagen, 2002). By recognizing this evolutionary dynamic, therapists can devise effective treatments to inform their patients, improve their condition, and forestall the destructive effects that such evolutionary dynamics may have upon patients and their significant others.

In conclusion, future investigations into familial friction and therapeutic treatments may benefit from an examination of interpersonal and intrapersonal conflict from the perspective of extended phenotypic manipulation. Such an evolutionarily-grounded investigation may improve upon earlier psychoanalytic discussions of familial conflict as expressed through unconscious processes. The

examination of unconscious family dynamics from an evolutionary perspective may prove useful in isolating and examining the manipulative behaviors that family members employ against each other and against themselves as a result of genetic conflicts of interest.

Evolutionary Ethics of the Family

In the final section of this chapter, we focus on the roles that arms races and mutual manipulation play in human ethics and morality. This will not be a discussion of what is moral or ethical. We do not offer prescriptions for proper moral conduct, as this is beyond the scope of the present chapter. In any case, the foregoing treatment of human adaptations to the family environment has shown how difficult it is to decipher moral rectitude and responsibility in a species that is rife with manipulative and deceptive tactics. Can genes or gene networks be held accountable for the actions of their phenotypic effects? Who (or what) has moral responsibility if individual actions are coded for by gene networks that transcend individual bodies? We believe that moral responsibility should not be sought on the genetic level. Whatever the genetic (or cultural) correlates of behavior are, judicial systems of deterrence and punishment are probably right to focus on the individual when assigning personal responsibility. While we should not excuse rape and murder by invoking biological motivations ("blame the genes!"), neither should we ignore the biological correlates of some of our most unsavory behaviors (for an excellent discussion of biology and moral responsibility, see Pinker, 2002).

Rather than devising methods for assigning genetic culpability, we discuss human morality from the perspective of evolved psychological mechanisms that seek to maximize the replication of the genes coding for their development. We also examine the social and cultural correlates of adapted moral sentiments whose ancestral domains were limited to family and tribal interactions. Ours is a tentative approach and may be more useful for the questions posed than for the answers provided. It is incumbent upon investigators in the biological, psychological, and social sciences to take the reins in this endeavor and to empirically flesh out these issues.

For any social species, the benefits of interacting with other members of their species must exceed the costs of going solo. There are a number of evolutionary explanations as to why organisms engage in cooperative relationships (see Trivers, 1985, for a review). The first is genetic relatedness and the mutual possession of genes "for" helping kin. Eusocial insects are notorious cooperators for this very reason and even put our own "family values" to shame. A second explanation for cooperation between organisms is based on the mutual exchange of favors, or reciprocal altruism (Trivers, 1971). For reciprocal altruism to evolve, organisms must repeatedly interact with one another and such interactions must persist for many generations. In these circumstances, the genetic interests of the interactants may be promoted through mutual cooperation. Provided that organisms gain a reproductive advantage over their entire cooperative period by cooperating with other reciprocators, immediate returns of favors are not necessary for the selection of general cooperative tendencies. What is necessary, however, is the ability to spot cooperators from non-cooperators, as cheaters may benefit by accepting favors without returning them. To guard against this threat, cooperators must evolve "cheater-detection" mechanisms to avoid and punish non-cooperators (see Cosmides & Tooby, 2005). This sets up an arms race in which cooperative strategies are pitted against non-cooperative or deceptive strategies across evolutionary time. As cooperators become better at detecting cheats, cheats should become better at deceiving and extracting resources from cooperators.

For humans, both kin favoritism and reciprocal altruism probably play a role in accounting for our sociality with respect to relatives as well as non-relatives [for a different explanation of human generosity and altruism, see Miller's (2000) account of sexual selection in humans]. Cooperation between kin may also involve reciprocity, and cooperation between non-kin may involve the redirection of modular processes for benefiting kin (see Qirko, Ch. 18, this volume). For most of human evolutionary history, our ancestors lived in small tribal societies based mostly on kinship ties. If two individuals from the same society were unrelated, chances were high that both were related to a third individual. It is therefore likely that our moral and empathetic sentiments had their origins in adaptive

acts of kindness directed towards individuals with whom genes "for" that kindness were shared. Likewise, the evolution of reciprocal altruism was enabled by the relatively small tribal societies within which individuals were forced into repeated interactions with their fellow tribesmen (the rudimentary forms of such cooperative structures can be witnessed in some of our great ape cousins—see Geary et. al., Ch. 21, this volume). With the increasing population density of early hominids, selection pressures came about that lead to the evolution of complex social dynamics. Our ancestors' cooperative and manipulative tendencies gained unprecedented reach as a result of these selection pressures, likely contributing to an increase in brain size and the evolution of language. With an increase in brain size came a prolonged developmental period and the need for parental and alloparental care. Children thus became increasingly dependent on their caregivers to acquire the knowledge needed to cooperate with and manipulate other individuals in their densely populated environments. Because humans are a cultural species (in that our evolved cognitive abilities are adapted to and express themselves within the contexts of rapidly changing informational and societal trends—i.e. language, technology, fashion, etc.), our evolved cooperative predispositions are dependent upon culturally acquired values and mores for their proper development. In this way, the development of human morality entails the adaptive attunement to certain familial and societal rules of conduct. Children's evolved learning mechanisms are specifically tuned to parental moral instruction early on in their development. This moral instruction was adaptive for children and parents alike in that children could learn the effective means by which to negotiate their social surroundings to mate and successfully replicate their parents' genes. When reflecting upon the dynamics of parent-offspring conflict, however, we are forced to admit that mutual benefit and cooperation is not all there is to moral instruction. Some familial rules of conduct may ultimately reflect extended phenotypic means by which individuals selfishly manipulate the behavior of their kin.

Extending biological and psychological findings to wider cultural phenomena is a risky endeavor. Human culture may function under rules and mechanisms that are unique to its domain. Nevertheless, human culture is a product of biological evolution and possesses an indelible stamp of its "lowly origin".

As such, we next examine the cultural expressions of our evolved moral sentiments to better understand how familial arms races and conflicts may play themselves out on our cultural stage. The tribal culture of our ancestors was different in many ways from our technologically interconnected global system. With advancements in transportation and communication technologies, the rate and extent of cultural change has been magnified to unprecedented levels. Taking into account this minefield of gene-culture coevolution, we limit our discussion and hypotheses to only a few societal trends. In doing so, we hope that researchers in diverse fields may apply some of these ideas to past and present societies across the globe.

If we are forced to define human culture, however tentatively, then we posit that culture entails the group-level expression of gene-level adaptations. Notwithstanding arguments for group-level selection, adaptation entails the selective retention of some alleles over others within a gene pool (Williams, 1966). The most salient vehicle of genetic expression is the individual organism, within which genes code for proteins in conjunction with other genes. On average, genes within an organism have been selected to cooperate with one another in building adaptations that are effective at propagating copies of those genes. Sometimes, however, genes can be selected at the expense of the other genes with which they share an organism, as in inclusive fitness or genetic imprinting, mentioned earlier. In humans, gene-level adaptations coding for individual-level psychological processes can be variously expressed as group-level cultural trends. In turn, group-level cultural trends may influence gene-level adaptations. Genes are still selected for how well they can replicate copies of themselves but some of those selection pressures result from the incidental group-level effects of genetic programs. Therefore, there is no need to invoke any kind of higher-level selection to explain cultural or genetic evolution. Certain societies may, however, be more successful than other societies as a byproduct of their culture, provided that certain cultural trends remain stable across generations and are more effective at promoting group survival than are other cultural trends. For example, whereas parents may violently discipline their

children in one society, another society's cultural practice of patient instruction and compassion may ultimately have more longevity.

Humans, like most mammals, possess a variety of adaptations for enhancing our reproductive opportunities. We likely employ psychological process to maintain sexual access to desired mates as well as to deceive and manipulate sexual rivals. Mate retention behaviors, for instance, may be used to prevent our sexual partners from abandoning us in favor of better reproductive opportunities. As mentioned earlier, such behaviors can be abusive as well as nurturing. To the extent that mate retention behaviors are employed to benefit one's genetic success, a certain amount of manipulation is inherent in such behaviors, even if they display generosity or compassion. Likewise, individuals can psychologically manipulate their sexual rivals via deception, as well as via intimidation and aggression. In both instances, strategies are employed to manipulate a sexual rival's behavior for one's own reproductive benefit. With the aid of language, humans may employ gossip and competitor derogation tactics to psychologically manipulate would-be mates away from sexual competitors—essentially manipulating the mate choices of their sexual targets in an extended phenotypic fashion, leading to the selection of genes that enable such manipulation (provided that the manipulation is evolutionarily successful). These tactics also vary by sex; because men more than women value physical attractiveness in a sexual partner, women are more likely than men to derogate their sexual competitors' appearance ("Look at her fat thighs!"). On the other hand, because women more than men value current or potential resource holdings in a sexual partner, men are more likely than women to derogate their sexual competitors' earning potential and lack of social standing ("He's not going anywhere in life!").

When applied to the moral systems of various cultures, manipulation of individuals for the sake of one's own reproductive interests is manifest on much larger scales. For example, men in polygynous societies whose wives reside in separate houses may lessen the threat of cuckoldry and sperm competition by requiring their wives or other men (their would-be sexual competitors) to undergo genital mutilation (Wilson, 2008). Whatever proximate explanations such cultural practices may have (i.e. religious,

aesthetic, initiatory, etc.), they may ultimately serve the evolutionary function of reducing paternity uncertainty and preventing investment in genetically unrelated offspring. If correct, Wilson's analysis may have uncovered evidence for culture-wide manipulative practices that are still prevalent in many societies, including our own. Depending on society, failure to comply with such rituals may lead to social ostracism or even death. A similar phenomenon may be at the bottom of culturally sanctioned monogamy and its social repercussions. The moral values associated with monogamy may reflect manipulative strategies by which genetically inferior men maximize their reproductive prospects by limiting the sexual opportunities of genetically superior men (Pinker, 1997). Female dress codes within certain Muslim societies may likewise be strategies by which men manipulate the sexual opportunities of their wives and other female family members. Likewise, women whose reproductive prospects are at stake may be complicit and even supportive of such practices if they can thereby reduce their competitors' genetic success. As is reflected by studies into parent-offspring conflict over mating decisions, families in such societies may exert control over their daughters' or sisters' sexual choices via the institution of arranged marriage and the threat of an "honor" killing if they fail to comply. The fact that such practices are so prevalent in Arab cultures may reflect the long history of agropastoralism within these societies (Apostolou, 2010). The accumulation of wealth that comes with agropastoralism may put pressure upon male resource holders to maintain their wealth and to prevent the squandering of their resources on relatives who reduce their genetic prospects with their mate choices.

Our psychological processes are amenable to a wide variety of cultural contexts and can creatively synthesize cultural information in novel ways, which may explain why our culture changes so rapidly. Although our genetic processes and familial conflicts are more or less predictable, their cultural expression varies across time and space. For example, the universal experience of parent-offspring conflict emerges through widely different cultural manifestations. The counter-culture movement of the 1960s, for instance, may have tapped into the psychological adaptations by which offspring counteract parental manipulation. Thus, the expression of "free love" may have been a culture-wide expression of

evolved mechanisms used by offspring to rebel against the influence of parents on their mating decisions. Likewise, the recent embracement of rap music and urban dress by white, suburban youths may reflect adaptive niche seeking behaviors by which individuals attract mates of their own choosing. In such instances, parental reproductive interests may be threatened by their offspring's free exercise of mate choice. Parents may in turn represent their genetic interests through their own cultural expressions. Conservative ideals and "family values" may be extended phenotypic manifestations by which parents attempt to influence offspring behavior by influencing social norms and morals. Further research is needed to track the specific design features of various cultural trends and examine the extent to which they reflect the evolutionary products of familial conflict. For example, parallels may be drawn between various youth and revolutionary movements and the adaptive behaviors by which offspring manipulate caregivers. Likewise, personality and familial-context factors can be examined for correlations with individual membership in various groups, religions, and political movements.

Thus, many of our modern rules of conduct may reflect the overextension of normally functional adaptations for enforcing morals and values upon family members to densely populated environments for which they were not selected. Our ancestors did not evolve in environments containing millions of densely packed humans sharing a radius of a few square miles, as in Tokyo and Manhattan. Although selection may have sped up with the onset of agriculture (as population growth brought about a higher genetic diversity on which selection could act—see Cochran & Harpending, 2009), an interconnected world of close to seven billion humans is historically unprecedented. The legal and judicial systems of modern states may reflect the co-optation of naturally or sexually selected moral sentiments to a much wider circle of interacting individuals. Thus, order and stability is achieved via the redirection of ancestral moral sentiments that were originally limited to intra-familial and reciprocal interactions. Although governments (often aided by state religion) can bring about smooth and efficient systems of cooperation and non-violent competition, they may also enforce rules and ordinances by which the reproductive interests of some individuals may be curbed for the benefit of others—usually those

enforcing the particular rules and ordinances. This may be a result of the overextension of manipulative adaptations by which humans attempt to influence the behavior of family members and unwary reciprocators. This is only to be expected if family members and other interactants possess traits for manipulating the behavior of their reproductive rivals, effectively utilizing their fellow humans as extended phenotypes of their own selfish genes. Our lives may be saturated with interconnected webs of manipulation by which some individuals or groups influence the behavior of other individuals or groups. Nowadays, these webs have grown to unprecedented complexity and reach with the aid of modern communication and transportation technologies.

Even though all humans possess adaptations for benefitting kin and cooperating with reciprocators, the cross cultural variation in morals, values, and taboos may reflect the wide variety of forms by which humans attempt to manipulate other humans in their environments. As touched on by Qirko (Ch. 18, this volume), religious and political systems may hijack our adaptations for benefitting kin into allocating investment to non-relatives by loading sermons, rituals, and political speeches with kin-based terms such as “brothers and sisters”. Likewise, our evolved tendencies to benefit those who may benefit us in the future may be taken advantage of by social systems that may never reciprocate (i.e. by promising heavenly rewards or utopian dreams). This is not to deny the potential reproductive benefits that individuals may enjoy by sacrificing on behalf of political or religious groups (Atran, 2002), but as with any cooperative relationship, there is always a risk of defection. Group-level systems of morality and ethics may reflect cooperative as well as manipulative adaptations, whether cognitive or emotional, by which individuals enforce rules of conduct upon their family members and acquaintances. Likewise, our adapted systems may be manipulatively subverted into pathways that are detrimental to our survival and reproductive prospects as easily as they can be co-opted for more benign purposes. For instance, evolved attachment systems that are usually directed toward caregivers may be activated by emotional pleas to “accept the love and guidance” of a “heavenly father” or a “holy mother” (see Kirkpatrick, 2004, for the application of attachment systems to supernatural agents). Similarly, manipulative adaptations

used to maximize one's inclusive fitness may transform into nepotistic moral systems that support royal families and other dynasties. Provided that parents and offspring can adaptively manipulate each other's behavior through discipline, moral instructions, and emotional expressions (as is expected from the theory of parent-offspring conflict), then ethical systems may reflect manipulative as well as cooperative forms of behavioral control that are extended to the wider society. Finally, evolved defenses against manipulation may be culturally expressed as consumer protection services, government regulations, and media-generated information campaigns. Scholars should not shirk the opportunity to uncover the extent to which societal laws, norms, and morals reflect cooperative, manipulative, and defensive extensions of human biological traits. Such an investigation can be especially fruitful if conducted with a proper evolutionary perspective.

Conclusion: Toward an Evolutionarily Enlightened Humanity

Our discussion of the evolutionary processes that underlie many of our interactions with family, friends, coworkers, strangers, and social structures and institutions, should not be interpreted as value judgments on these relationships. Even if there are manipulative adaptations which humans and non-humans employ in their dealings with other organisms, we may ultimately accept the manipulative nature of such relationships and continue to engage in them. For example, if our pets are ultimately co-evolved parasites that take advantage of our propensity to care for anything with infant-like features, should we then abandon our dogs and cats (see Archer, Ch. 16, this volume, but also see Paul & Serpell, Ch. 17, for possible health and reproductive benefits of pet-keeping)? Likewise, should we not adopt genetically unrelated offspring if adoption results from the misfiring of otherwise functional parental adaptations (see Volk, Ch. 8, this volume)? Such questions are absurd precisely because our evolved nature enables us to circumvent our genetic interests. Natural selection has provided us with adaptations that were successful at propagating our ancestors' genes, but only on average, and only within ancestral environments. It does not guarantee that we will always pursue the best way to spread our genes in the here and now, or even spread our genes at all. Such a realization has even eluded some scholars. A similar phenomenon, often

referred to as the naturalistic fallacy, is the mistaken assumption that explaining our biological nature is tantamount to an endorsement of it. If manipulating family members and friends for our own reproductive benefit is a result of evolved mechanisms and modules, should we then tacitly accept such manipulation as an unavoidable outcome of our evolutionary past? The selections within this volume are, in part, an attempt by researchers and scholars to tear down the veil of ignorance that enshrouds human nature. Only by understanding the evolutionary dynamics behind life's veneer can we hope to transcend our most sordid tendencies.

Of course we are not naïve. Overcoming our noxious predispositions may be a Sisyphean task. Our evolved capacities to deceive and manipulate one another may be unprecedented in their destructive potential. Nuclear, chemical, and biological weapons, nationalistic bigotries, religious fundamentalist threats, environmental degradation, and the power that communicative technologies provide for despots and demagogues intent on seducing the minds of millions, all speak to the dangers that our adapted mechanisms pose to our well-being. What gives us a sense of optimism, however, is the rapid advancement of human knowledge. By understanding evolutionary arms races and the nature of viruses and bacteria, we have been able to devise vaccines and cures for some of the deadliest diseases that have plagued humanity. With advancements in genetic engineering, we are able to feed millions of individuals with nutritious, calorie-rich foods. With market economies, we can bring about reciprocal relationships that transcend cultural, ethnic, racial, and national boundaries. With the aid of global communications systems, we can expand our circle of kinship and ingroup favoritism to include non-relatives and even non-human endangered species. With an increasing awareness of our environmental impact, we have begun to take steps to alleviate our destructive footprints upon this planet. The future, however, is far from certain.

As evolutionary scientists, our aim is to uncover the ultimate explanations for the proximate workings of our biological world. We hope that this volume accomplishes this task by stripping away some of the self-deceptive layers with which humanity has been clothed for millions of years. We spend

most of our lives interacting with kin. In understanding the evolutionary dynamics of the family, we believe that individuals can make more informed decisions regarding themselves, their kin, and their societies. Aside from such practical implications, we also hope that this volume instructs and enlightens those interested in the inner workings of human and non-human families. There is, however, much that remains undiscovered. It rests upon researches from diverse fields to correct many of our errors, oversights, and misconceptions. Empirical research is essential in corroborating or refuting the speculative nature of some of our inquiries. As with all of science, the study of human evolution is a work in progress.

References

Apostolou, M. (2009). Parent-offspring conflict over mating: The case of short-term mating strategies. *Personality and Individual Differences, 47,* 895-899.

Apostolou, M. (2010). Sexual selection under parental choice in agropastoral societies. *Evolution and Human Behavior, 31,* 39-47.

Atran, S. (2002). *In gods we trust: The evolutionary landscape of religion.* Oxford: Oxford University Press.

Bjorklund, D. F., & Pellegrini, A. D. (2002). *The origins of human nature: Evolutionary developmental psychology*. Washington, DC: American Psychological Association.

Brown, R. M., Brown, S. L., Johnson, A., Olsen, B., Melver, K., & Sullivan, M. (2009). Empirical support for an evolutionary model of self-destructive motivation. *Suicide and Life-Threatening Behavior, 39,* 1-12.

Buss, D. M. (1987). Love acts: The evolutionary biology of love. In R. J. Sternberg & M. F. Barnes (Eds.), *The psychology of love* (pp. 100-118). New Haven: Yale University Press.

Buss, D. M. (2003). *The evolution of desire: Strategies of human mating (revised edition).* New York: Basic Books.

Cochran, G., & Harpending, H. (2009). *The 10,000 year explosion: How civilization accelerated human evolution.* New York: Basic Books.

Cosmides, L. & Tooby, J. (2005). Neurocognitive adaptations designed for social exchange. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 584-627). Hoboken: Wiley.

Darwin, C. R. (1859/1964). *On the origin of species*. Cambridge, MA: Harvard University Press.

Dawkins, R. (1976). *The selfish gene.* Oxford: Oxford University Press.

Dawkins, R. (1982). *The extended phenotype.* Oxford: W. H. Freeman.

Hagen, E. H. (2002). Depression as bargaining: The case postpartum. *Evolution and Human Behavior, 23,* 323-336.

Hamilton, W. D. (1964). The genetical evolution of social behaviour (I and II). *Journal of Theoretical*

Biology, 7, 1-52.

Harris, J. R. (2009). *The nurture assumption: Why children turn out the way they do* (rev. ed.). New York: Free Press.

Kaighobadi, F., Shackelford, T. K., Popp, D., Moyer, R. M., Bates, V. M., & Liddle, J. R. (2009). Perceived risk of female infidelity moderates the relationship between men's personality and partner-directed violence. *Journal of Research in Personality, 43*, 1033-1039.

Kirkpatrick, L. A. (2004). *Attachment, evolution, and the psychology of religion.* New York: Guilford Press.

Lummaa, V., Vuorisalo, T., Barr, R. G., & Lehtonen, L. (1997). Why cry? Adaptive significance of intensive crying in human infants. *Evolution and Human Behavior, 19*, 193-202.

Maestripieri, D., Hoffman, C. L., Anderson, G. M., Carter, C. S., & Higley, J. D. (2009). Mother-infant interactions in free-ranging rhesus macaques: Relationships between physiological and behavioral variables. *Physiology & Behavior, 96*, 613-619.

Miller, G. (2000). *The mating mind: How sexual choice shaped the evolution of human nature.* London: Heineman.

Miner, E. J. & Shackelford, T. K. (2010). Mate attraction, retention, and expulsion. *Psichothema, 22*, 9-14.

Pinker, S. (1997). *How the mind works.* New York: Norton.

Pinker, S. (2002). *The blank slate: The modern denial of human nature.* New York: Viking.

Rousseau, J. J. (1755/1994). *Discourse upon the origin and foundation of inequality among mankind.* New York: Oxford University Press.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136-179). Chicago: Aldine-Atherton.

Trivers, R. (1974). Parent-offspring conflict. *American Zoologist, 14*, 249-264.

Trivers, R. (1985). *Social evolution.* Menlo Park, CA: Benjamin-Cummings.

Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary*

thought. Princeton, NJ: Princeton University Press.

Wilson, C. G. (2008). Male genital mutilation: An adaptation to sexual conflict. *Evolution and Human Behavior, 29,* 149-164.