

4 | Kindness, Fidelity, and Other Sexually Selected Virtues

Geoffrey Miller

Sexual Selection for Moral Virtues

Human good turns out to be the activity of the soul exhibiting excellence.

—Aristotle (*Nicomachean Ethics*, 350 B.C.)

We feel lust for other people's bodies, but we fall in love with their mental and moral traits. Many sexually attractive facial and bodily traits evolved to reveal phenotypic condition and genetic quality, including health, fertility, and longevity (Fink & Penton-Voak, 2002; Henderson & Anglin, 2003; Langlois, Kalakanis, Rubinstein, Larson, Hallam, & Smooth, 2000). This paper explores the possibility that our distinctively human moral traits evolved through sexual selection to serve an analogous display function. The most romantically attractive mental traits—intelligence, wisdom, kindness, bravery, honesty, integrity, and fidelity—often have a moral or quasi-moral status.

Recent empirical research suggests that many of these moral traits are sexually attractive and can serve as mental fitness indicators: they reliably reveal good mental health, good brain efficiency, good genetic quality, and good capacity for sustaining cooperative sexual relationships and investing in children (e.g., Alvard & Gillespie, 2004; Hawkes & Bird, 2002). Thus, the moral virtues that we consider sexually attractive are not culturally or evolutionarily arbitrary. Rather, they evolved to advertise one's individual fitness in hard-to-fake ways that can be understood through a combination of sexual selection theory (Andersson, 1994) and costly signaling theory (Zahavi & Zahavi, 1997).

This paper develops a theory that sexual selection shaped many of our distinctively human moral virtues as reliable fitness indicators. It updates and builds upon chapter 7 ("Virtues of Good Breeding") in my book *The Mating Mind* (Miller, 2000a) and emphasizes relevant empirical and

theoretical work since 2000. It tries to integrate person perception research with person-level approaches to moral philosophy, especially virtue ethics (Flanagan, 1991; Hursthouse, 1999; Pence, 1984; Stohr & Wellman, 2002) and naturalistic approaches to understanding moral intuitions (e.g., Nesse, 2001; Ridley, 1996).

The paper has twelve sections. First, it introduces the idea of sexual selection for moral virtues by considering the role of morality and romantic virtues in human courtship. Second, it emphasizes that this sexual selection model does not imply that morality is illusory, superficial, or covertly sexual. Third, it considers moral judgments of whole persons rather than isolated behavioral acts, in the general context of person perception, social attribution, and mate choice; this usefully blurs the distinction between “moral” virtues and other sexually attractive virtues such as intelligence, creativity, humor, charisma, bravery, mental health, physical health, strength, fertility, and beauty. Fourth, it reviews new “costly signaling” and “fitness indicator” models of sexual selection for “good genes” and “good parents” in relation to human altruism. Fifth, it explains how sexual selection in a socially monogamous species such as ours, with mutual mate choice, can result in minimal sex differences in the moral virtues. Sixth, it examines which specific moral virtues seem best explained by sexual selection. Seventh, it reviews evidence that the moral virtues really are sexually attractive to both sexes across many cultures. Eighth, it reviews behavior genetics evidence that the moral virtues and vices remain genetically heritable in our species, providing a continuing incentive for mate choice. Ninth, it examines moral and quasi-moral traits from the perspective of psychological research on individual differences in intelligence, personality, and psychopathology. Tenth, it considers how sexual selection may have interacted with other selection pressures (kinship, reciprocity, group selection, and equilibrium selection) to shape moral virtues. Eleventh, it identifies twenty testable empirical ways to assess whether particular moral virtues evolved through sexual selection, and it illustrates how to apply these assessments in the case of one specific virtue, sexual fidelity. Finally, this paper considers this theory’s sobering implications for the practice of normative ethics by philosophers (i.e., sexually mature human males and females whose moral intuitions have been shaped by millennia of sexual selection).

Romantic Virtues and Moral Virtues

This sexual selection theory of moral virtues may appear bizarre at first to moral philosophers and moral psychologists. From Saint Augustine through

Sigmund Freud, sexuality has been viewed as morality's nemesis. It was hard to imagine that virtues might arise through mate choice when Western thought was gripped by the traditional dichotomies of body versus spirit, lust versus virtue, and sinners versus saints. Also, most philosophers after Aristotle have focused on evaluating the morality of isolated acts rather than the moral virtues of whole people. This made it hard to view ethics as a branch of person-perception or individual-differences psychology. Even within evolutionary theories of morality, moral capacities have traditionally been seen as pragmatic tools to increase individual or group survival prospects rather than as costly, conspicuous signals to increase individual reproductive prospects.

To overcome these intellectual biases, it may help to take a step back and think about moral virtues in the context of real human mate choice. Apart from physical appearance and social status, which traits most excite our romantic impulses? People often fall in love based on (unconscious) assessments of each other's generosity, kindness, honesty, courage, social sensitivity, political idealism, intellectual integrity, empathy to children, respectfulness to parents, or loyalty to friends. The most romantic personal traits are often those that have been considered praiseworthy moral virtues by the world's most influential philosophical and religious traditions from ancient Greece, Israel, Arabia, India, China, and Japan. These lovable virtues overlap almost entirely with a combination of Nietzsche's (1887/1967, 1888/1968) "pagan virtues" (e.g., leadership, bravery, strength, skill, health, fertility, beauty, tolerance, joy, humor, and grace) and the traditional "Christian virtues" (e.g., faith, hope, charity, love, kindness, fairness, equality, humility, and conscience).

Moral virtues are, among other things, personal traits that we are proud to display during courtship. Indeed, courtship in most cultures can be viewed as a ritualized test of diverse moral virtues, such as kindness in gift giving and food sharing, conscientiousness in keeping dates and promises, empathy in talking and listening, and sexual self-control. Courtship is a moral obstacle course that we set up for each other, in which we test each others' generosity, sympathy, patience, fidelity, honesty, and etiquette. For courtship to be reliable, valid, and discriminating as a moral test, it must lead to a perceivable range of moral failures (e.g., broken promises, revealed prejudices, irritabilities, infidelities, impatient sexual pressures) that reflect an underlying distribution of stable moral character traits.

In prototypical romance stories across cultures, both characters fall in love, enjoy bliss, get lazy, make some moral errors, have a moral crisis, recognize their moral failures, resolve to improve their moral character, magnanimously forgive each other, and live happily ever after. It is not

romantic for characters to make and forgive purely perceptual failures (e.g., failures of depth perception or color constancy) or purely cognitive failures (e.g., base rate neglect or hindsight bias). If neither individual in a sexual relationship cares about projecting moral virtues (as in relations between prostitutes and clients, masters and slaves, or presidents and interns), then the relationship is considered superficial and unloving.

Our romantic emotions seem to amplify the subjectively perceived variance in moral character across potential lovers. When we fall in love, new lovers seem morally exemplary; when they make moral errors, they seem morally treacherous; when they make amends, they seem morally redeemed; when they divorce us, they seem morally repulsive. Borderline personality disorder (the tendency to view intimate partners in unstable, dichotomized ways, as extremely good or extremely evil—see Koenigsberg, Harvey, Mitropoulou, Schmeidler, New, et al., 2002) is just an exaggerated form of the normal human tendency to alternately overvalue and undervalue our lovers' virtues.

Conversely, moral vices are character flaws that we would be embarrassed to reveal to potential mates. These sexually embarrassing vices include not just obviously antisocial behaviors (killing, raping, lying, cheating) but also victimless addictions (sloth, gluttony, greed, envy, pride, drinking, smoking, drug taking, gambling, masturbating), failures of prosocial magnanimity (undertipping waiters, ignoring starving children, fleeing combat), and acts of symbolic meanness (kicking dogs, burning flags, cursing the gods). The common denominator in these moral vices is that they lead potential mates to hold our moral character in lower esteem, so they are less likely to breed with us. Across cultures, the leading causes of divorce (infidelity, abuse, addiction, unemployment—see Betzig, 1989) are almost all seen as serious moral failures. To many moral psychologists and philosophers, the sexual costs of moral vice may seem tangential to an evolutionary account of human morality. Yet to evolutionary biologists, a direct connection between moral vice and impaired reproductive success should be highly suggestive.

Sexually Selected Functions versus Sexual Motivations

To suggest that human moral virtues evolved through mate choice is not to suggest that morality is “really all about getting laid” at the level of individual motivation. Evolutionary functions must not be confused with proximate motivations (Richards, 2000). Just as sexual selection can produce genuinely beautiful peacock tails and genuinely creative

nightingale songs, it can produce genuine psychological altruism, not just fake generosity as a seduction tactic (Miller, 2000a). Most sexually selected adaptations do not include a little copy of their adaptive function inside themselves as a secret libidinous motive. Male beards and female breasts have no doubt been shaped by mate choice (Barber, 1995), but neither beards nor breasts need to contain any subconscious sex drive to remind them that they are supposed to be attractive.

Why does this distinction between adaptive functions and subjective motives seem so clear when we think about beards and breasts but so fuzzy when we think about moral behavior? Perhaps one reason is that we have evolved a high degree of wariness about being sexually exploited. Some people are sexually predatory and consciously produce behaviors that they know will be sexually attractive just to seduce us (Mealey, 1995; Wilson, Near, & Miller, 1996). If such a person admits that their apparently moral behavior was just aimed at fornication, we rightly get upset and worry that they are a Machiavellian psychopath. Some overgeneralize this response to stigmatize any evolutionary psychologists who try to identify any reproductive benefits for any form of altruism.

Evaluating Moral Persons versus Moral Acts

This paper considers moral judgments and moral virtues at a level of description that is still fairly unusual in moral philosophy—the level of whole persons, not isolated behavioral acts. It argues that much of human morality emerged through the co-evolution of our moral virtues as personality-type dispositions, and our social-cognitive adaptations for judging those moral virtues in others. This moral-person level of description is the domain of mate choice in evolutionary psychology, person perception in social psychology, virtue ethics in moral philosophy, parole decisions in criminal justice, and voter choice of political leaders in democratic elections. By contrast, the moral-act level of description is the domain of adaptive decision making in evolutionary psychology, social attribution in social psychology, act ethics in moral psychology, and guilt-or-innocence decisions in criminal law.

On this account, we rarely made moral judgments about isolated behavioral acts in prehistory. Rather, we made a hierarchy of inferences—about moral personality traits (virtues or vices) from behavioral acts, and about the ethical merit of whole persons from estimates of their moral personality traits. This is because we had to choose whether, when, and how to interact with a particular person as a whole package of morally valenced

personality traits. They could be favorite offspring or black sheep, friend or enemy, lover or ex-lover. We could not pick and choose our social interactions trait by trait.

Also, individuals' actions were probably assessed against the background of their age, sex, health, fitness, personality, intelligence, and other individual-differences dimensions, which jointly determine our expectations about their likely moral capacities. For example, we tolerate theft by toddlers more than theft by adults. We forgive unkind words spoken during high fevers by the sick. We do not expect a keenly empathic theory of mind in the severely brain-damaged or autistic.

Further, individuals' actions were probably assessed in the context of their actual social, sexual, tribal, and/or genetic relationships to us. Different social-interaction domains called for different moral-judgment criteria, focused on different virtues. In mate choice, we may give great weight to the virtues of intelligence, kindness, fidelity, and honesty, plus a few romantic virtues such as beauty, youth, and humor. By contrast, in kin altruism, we may give higher weight to the kinship-specific virtues of genetic similarity and expected future reproductive success, while caring little about kindness, gentleness, or honesty. This is why mothers can love psychopathic sons, and why fathers can love the selfish, screaming semiclones called babies. It is mainly in the domain of social reciprocity with unrelated acquaintances that we see the sort of tit-for-tat moral accounting that corresponds to the traditional moral philosopher's emphasis on the moral evaluation of isolated behavioral acts.

The moral-person level of description is different in some key respects from the moral-act level of description. First, we generally accept as a conversational implicature that "ought implies can" when we judge moral acts (Sinnott-Armstrong, 1984), but we do not necessarily follow this implicature in judging the morality of whole persons. That is, we typically do not expect someone to follow a normative moral principle (an "ought") in a particular behavioral instance if they cannot, due to some overwhelming external or internal constraint. We don't expect quadriplegics to jump in front of trolleys to save children, or crack addicts to vote conscientiously. However, when judging the morality of whole persons in real sociosexual relationships, we are rarely so forgiving. If a potential mate has Tourette's syndrome and can't refrain from screaming "Crack-head slut!" repeatedly in public during a first date, there is unlikely to be a second date, no matter how much we understand about verbal disinhibition in neurological disorders. If a potential hunting partner had a severe head injury that renders him too clumsy to hunt effectively, we may pity him

but will still exclude him from the hunt. When the fitness stakes are high, as in real sociosexual relationships, we hold people morally accountable even for faults that are not their own. If we did not, then we would be logically incapable of shunning even serial-rapist psychopaths, who, after all, must be a joint product of their genes, environment, and random developmental events (Dennett, 2003; Pinker, 2002).

Second, “morality” means something different at the person level compared to the act level. A moral act may be one that obeys some rationally defensible, universalizable, deontic or consequentialist principle. However, a moral person, from the point of view of a standard prehistoric hunter-gatherer, is someone who embodies prosocial virtues that make him or her a good mate, friend, relative, or trading partner. In economic terms, a moral person is one whose individual behavior brings “positive externalities” to their social relationships. In game-theory terms, a moral person is simply one who attaches positive utility to the welfare of others, such that they tend to play Pareto-dominant equilibria in mixed-motive games. In evolutionary terms, a moral person is one who pursues his or her ultimate genetic self-interest through psychological adaptations that embody a genuine, proximate concern for others (de Waal, 1997; Nesse, 2001). All three of these working definitions are descriptive rather than normative. They are each open to quantitative, empirical verification by measuring the net positive externalities, Pareto dominance, or proximate empathy levels manifested by individuals in real social interactions.

Costly Signaling Theory, Fitness Indicators, and Moral Virtues

Since about 1990, new theories concerning “costly signaling” have revolutionized the study of both sexual selection and human altruism (Gintis, Smith, & Bowles, 2001; McAndrew, 2002). Most animal communication is relentlessly narcissistic, advertising the signaler’s own individual species, sex, age, health, fertility, social status, phenotypic condition, and/or genetic quality (Bradbury & Vehrencamp, 1998). Only rarely do animals communicate any referential information about the external world. The trouble with self-referential signals is that often, animals have incentives to lie about themselves, in order to attract more mates, solicit more parental investment, or deter predators and rivals. Why should animals ever believe any self-referential signals produced by other animals?

Costly signaling theory offers a solution: if a signal is so costly that only high-health, high-status, high-condition animals can afford to produce it, the signal can remain evolutionarily reliable (Zahavi & Zahavi, 1997).

Almost any sort of fitness-related cost will work: matter, energy, time, or risk. For example, a peacock's tail is burdensome in all four senses: its growth and maintenance requires several hundred grams of mass, many calories, much time to grow, and much risk (it is harder to escape from peacock-eating tigers). Very often, the most complex, elaborate, and puzzling signals observed in nature are the result of sexual selection through mate choice (Darwin, 1871/1981). These sexual ornaments almost always impose high costs on the bearer, guaranteeing their reliability as indicators of condition and fitness.

This paper argues that many human virtues evolved through sexual selection as costly signals, as fitness indicators. This hypothesis has been advanced by a few previous researchers (e.g., Hawkes, 1991; Tessman, 1995), and its empirical testing has been one of the most active areas of evolutionary psychology and evolutionary anthropology in the last few years. Indeed, many prosocial behaviors that were assumed to arise through kinship or reciprocity are now thought to have emerged as costly signals of individual fitness, favored by social and sexual selection.

For example, it was often assumed that risky big-game hunting evolved because the best hunters could better feed their own offspring (Lee & DeVore, 1968). However, most hunted meat from big game is distributed too widely in hunter-gatherer clans for this paternal provisioning theory to work. Rather, recent research suggests that the most successful hunters are willing to provide the prosocial "public good" of hunted meat because they attract more high-quality female mates (Alvard & Gillespie, 2004; Hawkes & Bird, 2002; Smith & Bird, 2000).

Costly signaling theory has intellectual roots in many traditions and academic fields, some of which explicitly applied it to explain human morality. In the Hasidei Ashkenaz movement of thirteenth-century German Judaism, more difficult moral acts (e.g., charity when one is poor, forgiveness when one is righteously angry) were considered more praiseworthy. In Friedrich Nietzsche's (1887/1976) *On the Genealogy of Morals*, pagan virtues were considered attractive signals of health and power. In Thorstein Veblen's *The Theory of the Leisure Class* (1899/1994), conspicuous consumption and conspicuous charity were seen as hard-to-fake signals of wealth and social status. In mid-twentieth-century economics, corporate advertising was interpreted as a costly, conspicuous signal of market power to competitors and of corporate profitability to investors, rather than just a way to entice consumer purchases (Dorfman & Steiner, 1954). In 1970s biology, Amotz Zahavi (1975) viewed many animal traits and signals as hard-to-fake indicators of animal fitness.

Our mate preferences for moral virtues may be explained by costly signaling theory. If a young woman places a single's ad stating "SHF, 26, seeks kind, generous, romantic, honest man," we can translate this in evolutionary terms as "single Hispanic female, 26, seeks a healthy male of breeding age with a minimal number of personality disorders that would impair efficient coordination and parenting in a sustained sexual relationship, and a minimal number of deleterious mutations on the thousands of genes that influence the development of brain systems for costly, conspicuous, altruistic displays of moral virtue." Of course, the single's ad itself is not the costly signal—it is cheap and easy to fake. Rather, the ad identifies some desired moral virtues that would be hard to fake consistently during a lengthy courtship.

Sexually selected costly signals typically advertise two classes of traits: good genes or good parenting abilities (Iwasa & Pomiankowski, 1999; Kokko, Brooks, McNamara, & Houston, 2002). Different moral virtues might advertise one or the other or both. Good-genes indicators advertise general "genetic quality," which probably reflects having a low "mutation load" (Eyre-Walker & Keightley, 1999; Ridley, 2001). By favoring mates with a lower-than-average number of harmful mutations, sexually reproducing organisms can increase the expected survival and reproductive prospects of their offspring—even if their mate contributes nothing as a parent after fertilization (Houle & Kondrashov, 2002). Moral virtues may function as good-genes indicators by being difficult to display impressively if one has a high mutation load that impairs the precision of body and brain development. For example, displaying a sophisticated, empathetic social intelligence requires the development of a complex theory of mind, which might be easily disrupted by a variety of mutations associated with autism, schizophrenia, mental retardation, social anxiety, and language impairments (Baron-Cohen, 2000). Thus, a conspicuously expert level of empathy may function as a sort of neurogenetic warranty.

By contrast, good-parent indicators advertise phenotypic traits that help care for offspring, such as feeding them, grooming them to remove parasites, protecting them from predators, resolving sibling rivalries, and teaching life skills through play and practice (Hoelzer, 1989; Iwasa & Pomiankowski, 1999). Thus, a conspicuously empathic personality may also function as a good-parent warranty, guaranteeing the likely patience, kindness, protectiveness, playfulness, and conscientiousness that helps children thrive.

Sexual Selection without Large Sex Differences

In most of the other 4,600+ mammalian species, sexual selection acts much more strongly on males than on females, since females do almost all of the parental care, so have incentives to be much choosier about their mates than males are (Andersson, 1994). Humans are unusual in having evolved a mating/parenting system of intensive offspring care by both mothers and fathers (Geary, 2000; Kaplan, Hill, Lancaster, & Hurtado, 2000), which favors social monogamy (at least medium-term pair-bonded relationships with expectations of sexual fidelity). This, in turn, can favor mutual mate choice by both males and females (Kokko & Johnstone, 2002; Miller, 2000a). Of course, males are not very choosy about short-term sexual partners but become as choosy as females about committing to long-term serious relationships likely to produce children (Kenrick, Sadalla, Groth, & Trost, 1990). Thus, human mate choice is mutual, with both males and females choosing carefully when forming the long-term partnerships most likely to result in reproduction.

Sexual selection is not restricted to explaining sex differences; it can also explain sexual similarities in extravagant traits when mutual mate choice is at work (Miller, 2000a). These mutually-selected traits usually show at least some of the following criteria: (1) large differences even between closely related species (e.g., humans vs. other great apes), (2) full maturation only after puberty, (3) sexual attractiveness to both sexes, during at least some phases of mate choice, and (4) cultural embellishment through body ornamentation (for physical traits) or skill learning (for mental traits). The human morphological traits that evolved through mutual mate choice probably include long head hair, relatively hairless bodies, everted lips, and visible white scleras around the iris of the eye (Barber, 1995). The mutually selected human mental traits that show very low average sex differences include general intelligence, cognitive abilities for language, art, music, humor, and ideology, and many moral virtues (Miller, 2000a).

Thus, a sexual selection account of moral virtues absolutely does not imply that males evolve all the conspicuous virtues and females play the passive role of virtue assessment (cf. Darwin, 1871/1981). Rather, it implies that both sexes evolved the complementary adaptations for morality: moral virtues that tend to be displayed selectively in high-payoff social and sexual contexts, and person-perception mechanisms for judging the moral virtues of others.

Although this sexual selection model does not predict uniformly large sex differences across all moral virtues, it does predict some specific sex

differences that cannot be explained by other models. Human males face higher variance and skew in reproductive success, so are predicted to allocate more energy, time, and risk to mating effort, including costly, dangerous, public displays of moral virtue. For example, this model naturally explains why males are overrepresented among prosocial heroes who risk their lives to save unrelated strangers (Farthing, 2005; Johnson, 1996), and why males remain overrepresented in high-risk, underpaid, altruistic professions such as the police, fire, rescue, paramedic, and other emergency services.

Which Moral Virtues Can Be Explained by Sexual Selection?

The moral virtues most readily explained by sexual selection are those most clearly manifested in sexual courtship, in long-term sexual relationships, and in child rearing. Courtship generosity is the most obvious class of sexually selected moral behaviors. It has obvious parallels to “courtship feeding” by animals, in which “nuptial gifts” are given by males to females as good-genes indicators and good-parent investments (Vahed, 1998). Human courtship generosity would include altruism, kindness, and sympathy to the sexual partner, to his or her children from previous relationships (one’s stepchildren), and to his or her family members (one’s in-laws). Since this sort of courtship generosity is directed at nonrelatives and is not expected to be reciprocated, it is hard to explain through kin selection or reciprocal altruism, and it qualifies as evolutionary altruism by traditional definitions.

Courtship generosity may even include much of the paternal effort that is usually assumed to arise through kin selection (where “kin” include “offspring”), since most divorced fathers cut off their paternal investment as soon as they are cut off from sexual access to mothers (Anderson, 2000; Anderson, Kaplan, & Lancaster, 1999; Hofferth & Anderson, 2003). Thus, what looks like unproblematic paternal investment by males for the sake of perpetuating one’s genes in one’s children may turn out to be better described as ongoing courtship generosity by males in order to maintain sexual access to the mothers of those children.

Other sexually selected moral virtues may include sexual patience, sexual fidelity, and sexual generosity. Sexual patience is the opposite of sexual harassment, sexual stalking, and sexual coercion (rape). If a potential male mate shows a virtuous degree of sexual self-restraint throughout a long courtship period, this is valuable for several reasons. It does not compromise a woman’s power of mate choice, which is the foundation

of sexual selection. It reliably signals that the mate is not just looking for an opportunistic short-term affair but would value a longer term committed relationship. It also signals that the mate is not a sexually predatory psychopath and reveals efficient frontal-lobe control over limbic impulses.

Similarly, sexual fidelity is valuable for both practical and signaling reasons. Practically, fidelity minimizes the spread of sexually transmissible pathogens, the risk of cuckoldry (a male investing in offspring that were sired by another male), and the costs of polygyny (a female losing investment in her own children if a male sires children by another female). Sexual fidelity also carries much the same signaling power as sexual patience: attractive partners who remain faithful despite credible opportunities for extra-pair copulation are revealing that they expect the long-term relationship with one another to yield higher net fitness benefits than a series of short-term flings with others. That is, they treasure, value, and love one another above all others and have the self-control to remember that even in the face of temptation. Along these lines, although males are attracted to promiscuous females as potential short-term mates (Oliver & Sedikides, 1992; Schmitt, Couden, & Baker, 2001), neither sex respects high levels of promiscuity in potential long-term mates (Marks & Fraley, 2005; Milhausen & Herold, 1999; O'Sullivan, 1995).

Sexual generosity during foreplay and copulation certainly brings proximate benefits in terms of sexual pleasure, but that begs the ultimate, evolutionary question: why does successful mutual orgasm in humans require such a high degree of attentiveness, sympathy, communication, mind-reading, and previous experience with a particular partner? Other great apes, such as chimpanzees and bonobos, of both sexes, appear to reach orgasm without such an investment of time, energy, touch, and mindfulness (Anestis, 2004; Hohmann & Fruth, 2000). Only humans seem to have transformed copulation itself into a moral test of each partner's theory of mind (and theory of body). If orgasms came easily and often to us, they would be useless for discriminating altruistic partners from selfish partners, or good-genes partners from bad-genes partners (Miller, 2000a; Thornhill, Gangestad, & Comer, 1995). Just as human females are choosier early in courtship (in deciding whether to have sex) and human males become choosier later in courtship (in deciding whether to stick around after a bit of sex), female sexual excitement is hard to achieve early in courtship, and male sexual excitement is hard to achieve after the first few years of marriage (Clement, 2002). In each case, humans have apparently evolved an orgasm-resistant brain precisely to test partners' degree of

sexual altruism—that is, their ongoing level of commitment, patience, sympathy, and creativity.

A third class of sexually selected moral virtues may include ideological extremism among young adults, who are near the peak of mating effort. Adolescents and young adults often adopt social, political, and religious views that are more extreme than any they held before puberty and that become much less extreme in midlife after they settle down into stable monogamy and child rearing (Miller, 1996; Tilley, 2002; Visser & Krosnick, 1998). As young adults age, extreme and idiosyncratic attitudes tend to soften, increasing participation in mainstream elections, organized religions, and nonprofit charities. Conspicuous displays of ideological fervor (e.g., organizing political protests, leading revolutions) may function as reliable personality indicators. Under some oppressive regimes, they may also function as very high-risk heroic altruism indicators, especially among young males at the peak of mating effort. This may explain the moral fervor of the young Akhenaten, Buddha, St. Paul, Muhammed, Martin Luther, Thomas Jefferson, Karl Marx, Vladimir Lenin, Mao Tse-tung, Malcolm X, and Nelson Mandela—who all launched major ideological movements around age 30.

Precursors of many human moral virtues, such as empathy, fairness, and peacemaking, have been found in other great apes (de Waal, 1997, 2000; Preston & de Waal, 2002). My claim is not that sexual selection created our moral virtues from scratch in our species alone, without any primate foundation. Rather, my claim is that sexual selection amplified our standard social primate virtues into uniquely elaborated human forms.

Are the Moral Virtues Really Sexually Attractive?

The two largest cross-cultural studies of mate preferences have been coordinated by David Buss (1989) and David Schmitt (2004a, 2004b). Buss and his collaborators (1989) asked 10,047 people from 37 cultures to rate and rank order the desirability of several traits in a sexual partner. Among the top ten traits most desired by both men and women across almost all cultures were kindness, intelligence, exciting personality, adaptability, creativity, chastity, and beauty. Each of these has at least quasi-moral status in many cultures. Schmitt and collaborators (2004a, 2004b) gathered data on 17,804 people from 62 cultures and found that sexual promiscuity, infidelity, and “mate poaching” were predicted by low agreeableness, low conscientiousness, and high extraversion (Schmitt, 2004a, 2004b). Thus, three of the “Big Five” personality traits (Goldberg, 1990) carry a

sexual-morality valence that would be important in mate choice. Also, 49 out of 62 cultures (79%) endorsed a normative ideal of “secure” romantic attachment, as opposed to dismissing, preoccupied, or fearful attachment (Schmitt et al., 2004c). That is, most people in 79% of sampled cultures supported a moral ideal that couples should strive for a stable, low-conflict, high-mutual-valuation relationship. Also, many studies show that single’s ads across cultures often advertise and seek moral traits—especially kindness, generosity, honesty, fidelity, and capacity for commitment (e.g., Koziel & Pawlowski, 2003; Oda, 2001). Thus, morality and mate choice are tightly interwoven across human cultures.

In addition to these large-scale cross-cultural studies, research has confirmed that many particular moral virtues are sexually attractive and relationship stabilizing; these include the following:

- Kindness: emotional responsiveness to the needs of others (e.g., Jensen-Campbell, Graziano, & West, 1995; Karney & Bradbury, 1995; Li, Bailey, Kenrick, & Linsenmeier, 2002).
- Empathy: lovingness, affection, fondness, commitment, forgivingness, trust, and perspective taking (e.g., Miller & Rempel, 2004; Wieselquist, Rusbult, Foster, & Agnew, 1999).
- Niceness: emotional stability, conscientiousness, agreeableness, nonirritability, and nonviolence (Bouchard, Lussier, & Sabourin, 1999; Gottman, Coan, Carrere, & Swanson, 1998; Herold & Milhausen, 1999; Shackelford & Buss, 2000; Urbaniak & Kilman, 2003).
- Honesty (e.g., DePaulo & Kashy, 1998; Haselton, Buss, Oubaid, & Angleitner, 2005; Shackelford & Buss, 1996; Williams, 2001).
- Generosity to partner, children, and strangers (e.g., Buss & Schmitt, 1993; Goldberg, 1995).
- Capacity for self-control, self-respect, and self-disclosure (e.g., Byers & Demmons, 1999; Finkel & Campbell, 2001).
- Heroism (e.g., Farthing, 2005; Johnson, 1996; Kelly & Dunbar, 2001).

Of course, these moral-virtue preferences are typically stronger when seeking a serious long-term partner than a short-term lover (Herold & Milhausen, 1999; Scheib, 2001; Urbaniak & Kilman, 2003).

Apart from the sexual attractiveness of moral virtues, sexual competition seems to explain the evolution of many specific moral vices and antisocial behaviors. For example, most male violence, homicide, and warfare seem to reflect direct sexual competition for mates, for mating-relevant resources, and for mate-attracting social status (Daly & Wilson, 1988; Ellis, 2001; Summers, 2005). This probably explains the dramatic sex differences in

aggressive risk-taking across many domains (Byrnes, Miller, & Schafer, 1999) and the high rates of violence perpetrated by young males at peak mating effort across cultures (Daly & Wilson, 2001; Wrangham & Peterson, 1996). In males, testosterone seems important in organizing and activating these intrasexual competition adaptations, including aggressiveness, sensation seeking, risk seeking, and sexual motivation (Aluja & Garcia, 2005; Harris, Rushton, Hampson, & Jackson, 1996). Thus, testosterone could be construed as an “antivirtue hormone” in some sense. Over the longer term, many forms of intimate cruelty, such as derogating, abusing, and beating sexual partners, can be seen as “mate retention tactics” (Buss & Shackelford, 1997). Thus, sexual selection seems to explain not only the attractive, prosocial virtues (mostly through intersexual mate choice) but also the antisocial vices (mostly through intrasexual competition).

An apparent inconsistency arises: does human female choice really favor niceness or dominance, lovers or fighters, dads or cads? It seems to depend on the relationship context, the male’s sexual strategy, and the male’s other traits. Males who are low on “sociosexuality” (interest in multiple short-term matings) tend to project a “nice guy” image that is attractive for committed long-term relationships (Simpson, Gangestad, Christensen, & Leck, 1999). Male dominance is especially attractive when combined with a prosocial demeanor (Jensen-Campbell et al., 1995). Women seeking a long-term mate are more attracted to niceness, whereas women seeking a short-term mate are more attracted to physical appearance (Urbaniak & Kilman, 2003). By contrast, women at peak fertility, midcycle, when they would gain the greatest benefits from short-term good-genes mate choice, tend to prefer dominance to niceness (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004). As in other species, adaptive female choice requires an extraordinary sensitivity to the costs versus benefits of male dominance and aggressiveness—which can increase male intrasexual competitive ability and short-term sexiness but which also predict a male’s likelihood of using sexual coercion (Christopher, Owens, & Stecker, 1993).

Are the Moral Virtues Really Heritable?

If the moral virtues are favored as good-genes indicators, and if they are heritable, then sexual selection should favor them and increase their frequency in the population. Yet, if the virtues are driven to fixation (100% genetic prevalence) in the population, then there would no longer be any heritable variation in virtues, so the incentives for good-genes mate choice

would evaporate. Thus, we might expect good-genes mate choice to cannibalize the heritability of the traits that it favors. Is this a big problem for my model?

Actually, this is a special case of what biologists call the “lek paradox”: the puzzling fact that sexual ornaments remain conspicuously variable and heritable even when females choose males in large courtship-display congregations called “leks,” in which good-genes sexual selection is very strong. Biologists used to worry a lot more about the lek paradox, but they think there are some pretty good solutions now. For example, sexual ornaments may remain heritable because they are enormously complex and depend on many, many genes; sexual selection is constantly removing harmful mutations that have arisen in some of these genes, but new mutations are constantly arising in other genes (Rowe & Houle, 1996; Tomkins, Radwan, Kotiaho, & Tregenza, 2004). This mutation-selection balance maintains a large number of harmful mutations at equilibrium, on average. Yet it also tends to maintain a large variance in mutation load across individuals, and this is what keeps sexual ornaments heritable—why not all peacocks have equally spectacular tails, and why not all humans are equally virtuous.

This mutation-selection resolution of the lek paradox may sound fine in theory, but is there any evidence that the moral virtues are heritable in our species? There is much more behavior genetics work on the vices than on the virtues. Over 50 studies report substantial heritability for various forms of antisocial behavior and its personality correlates, such as psychopathy, sensation seeking, and disagreeableness (e.g., Agrawal, Jacobson, Prescott, & Kendler, 2004; Eley, Lichtenstein, & Moffitt, 2003; Jang, McCrae, Angleitner, Riemann, & Livesley, 1998; Krueger, Hicks, & McGue, 2001; Rhee & Waldman, 2002; Taylor, Loney, Bobadilla, Iacono, & McGue, 2003).

The heritability of prosocial virtues has been less well studied. Moderate heritability for altruism, empathy, nurturance, and/or responsibility has been found in a few twin studies (e.g., Beatty, Heisel, Hall, Levine, & La France, 2002; Davis, Luce, & Kraus, 1994; Zahnwaxler, Emde, & Robinson, 1992). For example, Rushton (2004) recently found moderate heritability for altruism, empathy, nurturance, and responsibility in 322 twin pairs. Several other morally relevant traits are known to be heritable, including social attitudes (e.g., conservatism, authoritarianism) and religiosity (e.g., D’Onofrio, Eaves, Murrelle, Maes, & Spilka, 1999; Koenig et al., 2005; McCourt, Bouchard, Lykken, Tellegen, & Keyes, 1999; Olson, Vernon, Harris, & Jang, 2001).

The general message from behavior genetics is that virtually every reliably measurable human behavioral trait shows a heritability of about .50, plus or minus .20 (Bouchard & McGue, 2003; Plomin, DeFries, McClearn, & McGuffin, 2001). We should not be surprised that the moral virtues fit this pattern, so there are continuing evolutionary incentives for good-genes mate choice based on moral virtues displayed in courtship.

Moral and Quasi-Moral Traits in Individual-Differences Psychology

The best studied individual differences dimensions in psychology—intelligence, personality traits, and psychopathologies—all have moral or quasi-moral status when they are assessed in social and sexual interaction. That is, the most important individual-differences dimensions are morally valenced, and their morally praiseworthy extremes increase sexual attractiveness.

Cognitive Traits

Intelligence (in the sense of general cognitive ability, the *g* factor, or IQ) is a morally valenced concept, which is why it has been so controversial throughout a century of psychometrics. In every domain of life, smart is good, and stupid is bad. This is not just because intelligence predicts objective performance and learning ability across all important life domains that show reliable individual differences (Jensen, 1998; Deary, 2000). It is also because having higher intelligence predicts many behaviors that we consider morally virtuous, such as being emotionally sensitive to the needs of others (Schulte, Ree, & Carretta, 2004), being an effective group leader (Judge, Colbert, & Ilies, 2004), working conscientiously (Gottfredson, 1997; Kuncel, Hezlett, & Ones, 2004; Lynn & Vanhanen, 2001), staying healthy through exercise and diet (Gottfredson, 2004; Gottfredson & Deary, 2004), and staying happily married (Gottfredson, 1997; Jensen, 1998). Conversely, having lower intelligence predicts many behaviors that most people consider morally objectionable, such as murder, rape, assault, alcoholism, drug addiction, absenteeism, child abuse and neglect, passing along sexually transmissible infections, and causing fatal traffic accidents (Gordon, 1997; Gottfredson, 1997; Lubinski & Humphreys, 1997). This may be one reason why intelligence is so attractive when both men and women consider potential long-term partners (Kenrick, Sadalla, Groth, & Trost, 1990; Li et al., 2002; Miller, 2000c).

One might object that intelligence is not really a “moral virtue”; it just happens to predict a wide range of specific moral behaviors. Yet, what is

a “moral virtue,” if not an individual-differences dimension, a psychological construct, an attributed trait, that predicts a wide range of specific moral behaviors? Moral virtues are socially attributed traits that carry predictive information about morally relevant behaviors. If kindness is a moral virtue because it predicts specific prosocial behaviors and is valued as such, then intelligence must also be a moral virtue—besides being an academic, economic, and epistemological virtue.

Personality Traits

Each of the Big Five personality dimensions (Goldberg, 1990) seems to have a moral valence that is positively correlated with its sexual attractiveness. These traits can be remembered with the acronym “OCEAN”: openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism.

Openness to experience implies intelligence, curiosity, tolerance, and broad-mindedness. It predicts emotional sensitivity (Schutte et al., 1998), social tolerance (Dollinger, Leong, & Ulicni, 1996), political liberalism (McCrae, 1996), and support for universalist values—the sort that would be supported by Kant’s categorical imperative (Roccas, Sagiv, Schwartz, & Knafo, 2002). People low in openness to experience tend to show unvirtuous traits such as being more prejudiced, racist, sexist, and anthropocentric, and higher on “right-wing authoritarianism” and “social dominance orientation” (Ekehammar, Akrami, Gylie, & Zakrisson, 2004; Heaven & Bucci, 2001; Van Hiel, Mervielde, & De Fruyt, 2004).

Conscientiousness implies fulfilling promises, respecting commitments, and resisting bad habits. It subsumes individual differences in industriousness, self-control, responsibility, and several other virtues (Roberts, Chernyshenko, Stark, & Goldberg, 2005). It predicts emotional maturity (McCrae et al., 1999), romantic lovability in relationships (Engel, Olson, & Patrick, 2002), team cooperation ability (Barrick, Stewart, Neubert, & Mount, 1998), and not killing people by driving safely (Arthur & Graziano, 1996). It also predicts prosocial civic and organizational engagement (Organ & Ryan, 1995; Penner, Dovidio, Piliavin, & Schroeder, 2005) and honesty, integrity, dependability, trustworthiness, and reliability at work (Sackett & Wanek, 1996). Further, conscientiousness positively predicts virtually every health-related behavior that increases longevity, including eating a healthy diet, exercising, and avoiding tobacco, excessive alcohol, addictive drugs, risky sexual behavior, risky driving, and suicide (Bogg & Roberts, 2004). Conscientiousness is also closely related to the capacity for self-control, which is a key virtue. Prefrontal brain damage, as in the

famous case of Phineas Gage, tends to reduce conscientiousness and disinhibits impulsive antisocial behavior, so it reduces both moral virtue and long-term sexual attractiveness.

Extraversion implies gregariousness, social intelligence, self-esteem, and leadership—some Nietzschean pagan virtues. It predicts prosocial volunteerism (Carlo et al., 2005) and happiness and optimism (Furnham & Cheng, 1999; Lucas, Diener, Grob, Suh, & Shao, 2000). However, extraversion is closely related to social attention seeking (Ashton, Lee, & Paunonen, 2002), so depending on whether virtue or vice attract more attention, extraversion may be associated with prosocial or antisocial behavior.

Agreeableness implies kindness, sympathy, and nonaggressiveness; it predicts benevolence and respect for moral traditions (Roccas et al., 2002), the quality and peacefulness of social relationships (Asendorpf & Wilpers, 1998), and success in jobs requiring teamwork and social interaction (Mount, Barrick, & Stewart, 1998). It is probably the most morally valenced of all the Big Five traits, with conscientiousness a close second.

Emotional stability (the opposite of neuroticism and anxiety) implies dependability, maturity, confidence, self-control, and equanimity. It strongly predicts happiness (DeNeve & Cooper, 1998), which is sexually attractive. It also predicts marital satisfaction in many studies (e.g., Caughlin, Huston, & Houts, 2000). Emotional stability is also related to the “secure attachment” style that predicts stability, intimacy, and fidelity in sexual relationships (Allen & Baucom, 2004; Bogaert & Sadava, 2002) and that is valued across cultures (Schmitt et al., 2004c).

All of the morally positive, socially desirable ends of the Big Five dimensions tend to be valued in mate choice and marital satisfaction (Berry & Miller, 2001; Botwin, Buss, & Shackelford, 1997; Bouchard et al., 1999; Donnellan, Conger, & Bryant, 2004). Mate choice for the Big Five traits may reflect both good-genes and good-parent effects. All of the Big Five are moderately heritable (Plomin et al., 2001). Yet good parenting ability is also positively predicted by openness, conscientiousness, extraversion, agreeableness, and emotional stability (Kochanska, Friesenborg, Lange, & Martel, 2004; Metsapelto & Pulkkinen, 2003; Spinath & O'Connor, 2003).

Psychologists typically avoid morally evaluative labels for personality traits, to avoid mixing descriptive science with normative ethics. However, one can remain perfectly descriptive by stepping back and considering person perception as a morally evaluative function of social cognition: our social-attribution systems tend to attribute moral valences to most personality traits when we observe them in other people. Indeed, this is one

reason for the runaway success of the Implicit Association Test in recent social cognition research: it reveals the deeply evaluative nature of implicit person perception (Greenwald et al., 2002).

Moral philosophers have lately rediscovered the old social psychology critiques of personality psychology, as in the “person versus situation” debate (Mischel, 1968) and work on the “fundamental attribution error” (Ross, 1977). Social psychology’s concern was that apparently stable personality traits may not really exist but may be projections of a biased social-attribution system. Citing this literature, Gilbert Harman (1999b, 2000b) argued that virtue ethics cannot succeed because social psychology shows there are no stable personality traits that could correspond to virtues. Unfortunately, virtue ethicists have usually responded to Harman’s critique with rather weak theoretical arguments (e.g., Merritt, 2000; C. Miller, 2003) rather than by citing the now well-established reliability, validity, stability, and heritability of personality traits (Funder, 2004; Matthews, Deary, & Whiteman, 2003) across cultures and even across species (Gosling, 2001; King, Weiss, & Farmer, 2005). Also, there have been some incisive critiques of situationist research in social psychology (e.g., Andrews, 2001; Sabini, Siepmann, & Stein, 2001) that may undermine some of Harman’s grounds for concern.

Psychopathology Traits

All major psychopathologies tend to increase perceived selfishness and to decrease perceived moral virtue, sexual attractiveness, and social status (McGuire, Fawzy, & Spar, 1994; Wakefield, 1999). This seems especially true for the most common and severe psychopathologies, such as psychopathy, major depression, and schizophrenia (Nesse, 2000; Shaner, Miller, & Mintz, 2004; Wilson et al., 1996). Many personality disorders, such as paranoid, narcissistic, and borderline disorders, also predict anti-social behavior (Coid, 2003). Signs of mental illness typically lead to social and sexual rejection by others—that is, to stigmatization through negative social attributions (Corrigan, 2000; Crisp, Gelder, Rix, Meltzer, & Rowlands, 2000). Serious mental illness almost always reduces reproductive success by reducing sexual attractiveness (Avila, Thaker, & Adami, 2001; Haukka, Suvisaari, & Lonnqvist, 2003). The only exception seems to prove the rule: the manic phase of bipolar disorder (“manic-depression”) often leads to increased magnanimity, heroism, gift giving, and moral crusading and also leads to new love affairs, infidelities, promiscuity, and babies (Jamison, 1993; Wilson, 1998).

Religiosity

In most hierarchical, large-scale societies throughout history, religion has provided a cultural framework for the display and evaluation of moral virtues. Yet in all societies, there are conspicuous individual differences in public religiosity (e.g., frequencies of churchgoing, tithe giving, public prayer) and in private faith. Psychology of religion research has shown that, although cultural and family environments determine specific religious affiliations, beliefs, and rituals, religiosity as an individual-differences trait shows moderate heritability that increases through adolescence to adulthood (D'Onofrio et al., 1999; Koenig et al., 2005). Religiosity also shows mild positive correlations with agreeableness, conscientiousness, and extraversion (Saroglou, 2002). It positively predicts moral conservatism, traditionalism, benevolence, and conformity and negatively predicts hedonism, status striving, and universalism (Saroglou, Delpierre, & Dernelle, 2004). There is strong assortative mating not only for specific religious affiliation but also for religiosity (Feng & Baker, 1994; Kalmijn, 1998).

Other Psychological Traits

There are many other traits that show both sexual attractiveness and a quasi-moral status, at least in a substantial proportion of societies. These include the capacities for the following:

- Creativity (Haselton & Miller, in press; Kanazawa, 2000; Miller, 1997, 1999).
- Artistic virtuosity (Boas, 1955; Kohn & Mithen, 1999; Miller, 2001).
- Achieving social status through merit (Ellis, 2001; Pérusse, 1993).
- Acquiring wealth through merit (Conniff, 2002; Frank, 1999; Veblen, 1899/1994).

Even if some critics insist on a narrower list of “true” moral virtues, these core virtues may still be explained by this sexual selection model. Kindness, for example, would surely be on any reasonable list of the core virtues, and it appears to fit the standard pattern of sexually selected traits given mutual mate choice: reliability as a stable personality trait, validity as a good-genes and good-parent indicator, heritability, sexual attractiveness in long-term relationships, and conspicuous display in courtship. Thus, for purposes of assessing this sexual selection mode, it may not matter much exactly where we draw the line between moral and nonmoral virtues.

Are These Traits Really Judged as Moral Virtues or Vices?

In what sense do these cognitive, personality, and psychopathology traits have a “quasi-moral status”? There are at least four reasons to think they do—three from social psychology and one from theology. First, most people show a “just world belief” (Lerner, 1980) that creativity, beauty, status, and wealth are merited by those who enjoy them, as both causes and consequences of moral virtue. Second, there is a powerful “halo effect” around such traits, so they are judged as boosting the likely moral virtues of judged individuals (Nisbett & Wilson, 1977). For example, defendants in criminal cases who are more physically attractive, high in occupational status, and wealthy are more likely to be acquitted or given lighter sentences by juries of their (often lower status) peers (McKelvie & Coley, 1993). Some halo effects may reflect accurate inferences about genuinely correlated traits (“true halo”) rather than perceiver bias (“halo error”) (Solomonson & Lance, 1997). Third, research using the Implicit Association Test shows that many dimensions judged in person perception are highly evaluative and load on a common good/bad dimension that confounds moral goodness, likeability, pleasantness, status, racial similarity, and physical attractiveness (Fazio & Olson, 2003; Greenwald et al., 2002).

Finally, the theological reason: religious people often attribute these quasi-moral traits in hypertrophied form to deities as a reason for valuing their goodness, as when they feel gratitude to a God credited with creating the world in all its beauty, out of a magnanimous generosity to mortals (Boyer, 2001; Roes & Raymond, 2003). Believers typically credit benevolent deities with supernatural levels of the quasi-moral personality traits (intelligence, conscientiousness, agreeableness, and emotional stability), as well as the standard sexually selected fitness indicators (size, strength, status, beauty, longevity). In monotheistic religions, these traits are bundled together; in polytheistic religions (e.g., ancient Egyptian, Greek, Roman, Norse, and Aztec pantheons; Hinduism, Confucianism), different supernormal traits are attributed to different deities. Contemporary comic books and fantasy films show the standard polytheistic pattern, with different supernormal quasi-moral traits attributed to different superheroes (e.g., the Marvel comics *X-Men* pantheon of Professor X, Wolverine, Cyclops, and Storm; the Tolkien pantheon of Gandalf, Aragorn, Legolas, and Frodo).

Ever since Socrates, philosophy has tried to develop precise distinctions between theoretical constructs that are often empirically correlated. Most philosophers think in terms of necessary and sufficient conditions, not in terms of factor analysis. Thus, moral philosophers may balk at such

flagrantly irrational conflation of moral goodness, social reputation, economic power, and sexual attractiveness. Indeed, they may be tempted to quote a cautionary verse from Ogden Nash: “It’s always tempting to impute/Unlikely virtues to the cute.” But moral philosophers did not drive the genetic evolution of human virtues; ordinary folks did. If we are seeking a descriptive explanation for human morality, we should attend to the person-perception judgments that may have causally driven moral evolution in our species. Ultimately, it is an empirical psychological question whether ordinary folks judge these traits to have a moral or quasi-moral status, especially in making social and sexual judgments about others.

Virtue Ethics, Virtue Epistemology, and Virtue Aesthetics

One reason for accepting the quasi-moral status of individual-differences traits such as intelligence and physical attractiveness is the recent convergence between virtue ethics, virtue epistemology, and virtue aesthetics. Philosophers are once again considering the relationships between goodness, truth, and beauty.

For example, there is clear overlap between virtue ethics and virtue epistemology, which is the study of cognitive and intellectual virtues (DePaul & Zagzebski, 2003). Traditional epistemology focuses on evaluating the truth of particular concepts and conceptual systems through consistency and coherence criteria. By contrast, virtue epistemology tries to understand the normative properties of beliefs in terms of the normative properties of cognitive agents. For example, Aristotle named intuition, wisdom, prudence, and science as intellectual virtues. For the virtue epistemologist then, true beliefs arise out of acts of intellectual virtue—acts typical of intelligent, rational, cognitively complex agents (Zagzebski, 1996) who show impartiality, epistemic responsibility, and intellectual courage (Code, 1987; Montmarquet, 1993). In virtue epistemology as in virtue ethics, the favored level of description is the whole individual as a cognitive/moral agent, not the isolated belief or moral act. This naturally leads to an emphasis on individual differences in epistemological virtue—differences that intelligence researchers have already succeeded in measuring with unparalleled reliability and validity for over a century.

Virtue epistemology and virtue ethics also strive for a unified theory of value across moral and cognitive domains (Brady & Pritchard, 2003). For Montmarquet (1993) the key intellectual virtue of “epistemic conscientiousness” resembles a moral personality trait more than a cognitive ability, and it seems closely related to the Big Five traits of openness and

conscientiousness. Kvanvig (1992) views intellectual virtues as cognitive ideals valued by people in social groups, thus relating virtue epistemology to person-perception research. Zagzebski (1996) has gone furthest in viewing the intellectual virtues as a subset of the moral virtues. Thus, if truth, knowledge, and accuracy are epistemological virtues, perhaps they are moral virtues as well. As with moral virtues, there is a strong distinction in virtue epistemology between getting things right accidentally versus intentionally: praiseworthy beliefs are those that are due to an individual's own abilities, efforts, actions, and skills rather than dumb luck or blind chance (Greco, 2000; Lehrer, 2000). In summary, virtue epistemology would see mate choice for intelligence as mate choice for a cardinal moral virtue.

Likewise, there is an evolutionarily deep relationship between moral goodness and aesthetic beauty, as reflected in the overlap between virtue ethics and the recent revival of Darwinian aesthetics (Grammer, Fink, Moller, & Thornhill, 2003; Miller, 2001; Thornhill, 1998). This has intellectual roots in late nineteenth-century evolutionary biology, when mate choice for sexual ornaments was seen as the central evolutionary process that creates organic beauty (Darwin, 1871/1981; Grosse, 1897; Spencer, 1887). Darwinian aesthetics is a virtue aesthetics insofar as it views beauty prototypically as an agent-level property of living organisms, as they are perceived by other members of the same species.

Beauty is thus an emergent property of coevolution between a signaling system (the beauty cues displayed by some individuals) and a receiver system (the aesthetic judgment system in other individuals). It is partly in the objective genetic quality and phenotypic condition of the beautiful individual and partly in the perceptual adaptations of the beholder (Senior, 2003; Symons, 1995). Darwinian aesthetics has successfully analyzed human facial and bodily attractiveness in costly signaling terms as a set of good-genes and good-phenotype indicators (e.g., Fink & Penton-Voak, 2002; Grammer et al., 2003; Langlois et al., 2000).

Darwinian aesthetics extends well beyond an animal's physical attractiveness. Art, music, and performances produced by animals (e.g., bowerbird nests, nightingale songs, hominid hand-axes, Cindy Sherman's self-portraits) can all be viewed as part of the organism's "extended phenotype" (Borgia, 1995; Dawkins, 1982; Kohn & Mithen, 1999). Such aesthetic behavioral products may be assessed by somewhat different perceptual adaptations than physical attractiveness, but they obey the same basic principles of costly signaling theory, such as conspicuous cost and conspicuous precision (Boas, 1955; Miller, 2001).

The question remains: is there any substantive overlap between virtue ethics and virtue aesthetics, such that beauty in the Darwinian-aesthetic sense could be construed as a genuine moral virtue? There are a few examples of beauty serving as a reliable cue of altruism. First, some sexually selected beauty advertises ability and willingness to invest resources in mates and offspring—that is, to perform acts of unselfish altruism in the interests of one’s family (Iwasa & Pomiankowski, 1999; Kokko, 1998). This good-parent sexual selection process favors the bright red plumage of male cardinals (Linville, Breitwisch, & Schilling, 1998), the dark chest-badges of male house sparrows (Voltura, Schwagmeyer, & Mock, 2002), and the aesthetically conspicuous resource displays of humans (Conniff, 2002; Miller, 2001). Second, some recent research confirms nineteenth-century criminologist Cesare Lombroso’s view that convicted felons (i.e., individuals low in virtue) tend to be less physically attractive than average. For example, adult felons, violent juvenile delinquents, and antisocial children show increased “minor physical anomalies,” craniofacial abnormalities, and neurodevelopmental abnormalities and decreased body symmetry, “developmental stability,” and overall attractiveness (e.g., Arsenault, Tremblay, Boulerice, Seguin, & Saucier, 2000; Harris, Rice, & Lalumiere, 2001; Lalumiere, Harris, & Rice, 2001). Finally, some recent philosophical work considers the intersection of aesthetics and ethics (Eaton, 1992; Levinson, 1998). For example, McGinn’s (1997) “aesthetic theory of virtue” argues that virtue coincides with “beauty of the soul,” and vice with ugliness of the soul.

The good, the true, and the beautiful are closely related—not because they share some conceptual overlap of necessary and sufficient conditions but because, in the real world, each tends to be disrupted by the same kinds of genetic mutations, developmental errors, and neuropsychological abnormalities. The result is that human moral virtues, cognitive abilities, and sexually attractive traits tend to positively correlate with each other across individuals.

How Sexual Selection May Have Interacted with Other Selection Pressures to Shape Human Moral Virtues

Many forms of social selection probably shaped human morality, including the following:

- Kin selection (Hamilton, 1964; Daly, Salmon, & Wilson, 1997).
- Reciprocal altruism (Trivers, 1971; Sugiyama, Tooby, & Cosmides, 2002).

- Commitment mechanisms (Frank, 1988; Nesse, 2001).
- Risk-sharing mechanisms (Boone, 1998; Sugiyama & Sugiyama, 2003).
- Social norm and punishment mechanisms (Fehr & Fischbacher, 2004; Henrich & Boyd, 2001).
- Group selection (Boehm, 1996; Wilson, Timmel, & Miller, 2004).
- Equilibrium selection among alternative evolutionary strategies (Alvard & Nolin, 2002; Boyd & Richerson, 1990).

In each case, sexual selection would tend to anticipate, sharpen, and amplify the social selection pressure to produce a more extreme, more costly, more prosocial version of the moral virtue than social selection could achieve alone. The reason is that nonsexual forms of social selection can shape morality only insofar as they confer fairly concrete survival benefits (e.g., shared food, protection from predators) on the morally virtuous. Mate choice can shape morality much more powerfully and broadly, because it demands only that moral behaviors carry some signaling value about a potential mate's good genes and/or good parenting abilities. In general, sexual selection can "supercharge" other evolutionary processes by adding just the sort of positive-feedback dynamics that tend to trigger evolutionary innovation and speciation (Crespi, 2004; Miller & Todd, 1995).

An especially interesting, powerful, and neglected interaction may be that between sexual selection and group-level equilibrium selection (not to be confused with standard group selection—see Miller, 2000a). Many evolutionary games have multiple "Nash equilibria": states where each player is maximizing their individual payoffs given the strategies already played by others. For example, male cetacean mating strategies have at least two equilibria: peacefully attracting females through long, loud songs (as in the humpback whales) or aggressively herding and raping females (as in the bottlenose dolphins—Connor, Smolker, & Richards, 1992). Some equilibria are better for everybody (they bring net positive payoffs to everyone; they are "Pareto dominant"); some equilibria are worse for everybody ("Pareto inferior") but cannot be escaped easily because individuals who deviate from the equilibrium do even worse. A virtuous bottlenose dolphin could not opt out of his species' coercion-based mating system without negating his reproductive success.

Normally, natural selection alone is not very good at escaping from such Pareto-inferior equilibria to reach Pareto-dominant equilibria (Boyd & Richerson, 1990). Sexual selection may help, by conferring reproductive benefits on individuals who deviate from selfish, antisocial equilibria

(Miller, 2000a). This sexual payoff for virtue is functionally similar to the social-reputation payoffs for virtue modeled by other researchers (e.g., Barclay, 2004; Milinski, Semmann, & Krambeck, 2002). However, standard social-reputation models create a second-order “free-rider” problem (Gintis, 2000): who will altruistically take the trouble to punish the wicked and reward the virtuous? As research from behavioral game theory (e.g., on the Ultimatum Game) shows, most humans are emotionally compelled to impose this sort of “altruistic punishment” of others who act selfishly (Fehr & Gächter, 2002); the question is why? Most explanations make somewhat vague appeals to cultural evolution or social norms (e.g., Boyd, Gintis, Bowles, & Richerson, 2003) without identifying any plausible individual fitness payoffs for punishing the wicked. By contrast, this sexual payoff model solves it by identifying selfish mate-choice incentives (e.g., good-dad and good-gene payoffs) for “rewarding” the virtuous with sexual relationships.

Most contemporary theories of moral evolution accept the importance of multilevel selection across the genetic, individual, and group levels—either implicitly or explicitly (Wilson et al., 2004). Generally, group-level selection for prosocial behavior is what “breaks the symmetry” between alternative equilibria in evolutionary games to allow the evolution of genuine empathy and altruism (Lahti & Weinstein, 2005). This model of sexual selection interacting with group-level equilibrium selection is a potent way that prosocial virtues can establish a genetic beachhead in an otherwise selfish population, long before group-level equilibrium selection can favor morally unified groups.

Predictions of the Sexual Selection Model for Moral Virtues

This sexual selection model makes a large number of testable predictions. These often take an unusual form, since costly signaling adaptations have very different phenotypic and genetic features compared to other types of adaptations. In particular, many of these predictions concern individual differences in virtues—not a common research topic in evolutionary psychology or moral philosophy, which tend to focus on species-typical moral judgments and behaviors. For more detail on the rationale behind these predictions, see Miller (2000a, 2000b, 2000c, 2001).

To test most of these predictions, it would be necessary to develop reliable, valid measurement scales that can identify stable individual differences in particular kinds of moral virtues. Such scales should ideally show the psychometric properties desired of any intelligence test or personality

assessment: internal consistency reliability, parallel-forms reliability, test-retest reliability, interrater reliability, face validity, construct validity, predictive validity, concurrent validity, convergent validity, discriminant validity, and ecological validity (Anastasi & Urbina, 1997). To discriminate between rival theories concerning the evolutionary origins and adaptive functions of specific human virtues, we need to assess the adaptive design features of each putative virtue in reliably quantitative ways. This will require much more psychometrically sophisticated approaches to virtue ethics—not just asking people to give answers to a few multiple-choice “trolley problems” from moral philosophy.

Generally, sexually selected virtues as quantified in this way should show most of the following twenty features:

Genetic Features

1. Positive heritability: if virtues are good-genes indicators, they should prove genetically heritable in twin and adoption studies or using other behavior-genetic methods. If virtues are costly and evolved under sexual selection, the genes underlying virtues should become more expressed only after sexual maturity, perhaps in response to sex hormones. This should lead to higher virtue heritability in adults than in children, as has been found with intelligence (Plomin et al., 2001).
2. Negative correlations with mutation load (number of harmful genetic mutations): heritable variation in virtues should reflect variation in overall mutation load, as intelligence may do (Prokosch, Yeo, & Miller, 2005). For example, since mutation load in sperm increases dramatically as men age (Crow, 2000), younger fathers should, all else being equal, sire more virtuous children.
3. Genetic inbreeding effects: if virtues are good-genes indicators, the offspring of sibling or cousin marriages should show reduced virtue levels, due to the increased expression of harmful homozygous mutations.
4. Molecular genetic features: specific virtue-reducing alleles should be mostly of fairly recent evolutionary origin that have not yet been eliminated by sexual selection in particular breeding populations; thus, despite the heritability of virtue, it will be extremely difficult to find specific “virtue genes” that replicate across human groups (see Shaner et al., 2004).
5. Positive genetic correlations between trait and preference: if mate choice was shaping virtues over recent evolutionary history, we should expect to see a positive genetic correlation between virtues themselves and choosiness about virtues. Such genetic correlations can be assessed with standard

multivariate genetic modeling, based on the cross-trait, cross-twin correlations in identical versus fraternal twin pairs.

Phenotypic Features

6. Stable phenotypic variance: virtues should vary significantly between individuals in the species, and the differences should be fairly consistent across situations (cf. Harman, 1999b). Without variance, there is no way for mate choice to use the trait as an indicator; without stability, there is no way to generalize the trait from one situation to another.

7. Condition-dependent costs: virtues should incur a significant cost to produce, in energy, time, risk, or nutritional resources. Individuals with higher genetic fitness or better phenotypic conditions should be better able to bear these costs.

8. Positive correlation with other objective fitness indicators: variation in virtues should correlate positively with other well-established fitness indicators, such as physical health, mental health, longevity, fertility, body size, body symmetry, and intelligence (e.g., Gangestad & Thornhill, 1999; Prokosch et al., 2005)

9. Comorbidity among vices, and between vices and brain abnormalities: if different virtue deficits (vices) reflect harmful pleiotropic mutations with partly overlapping effects, then vices should show positive genetic correlations (genetic comorbidity) with each other, especially as vices become more serious and extreme. Also, if vices reflect harmful mutations that impair normal neurodevelopment, then they should be associated with various standard brain abnormalities widely observed for other fitness-reducing behavioral traits such as mental illness and mental retardation: smaller cortical volume, larger ventricles, abnormal cortical lateralization, atypical localization of processing as observed in functional magnetic resonance imaging studies, and so forth.

10. Higher trait variance in males: in species that evolved with some degree of polygyny and some frequency of extra-pair copulation, the higher male variance and skew in reproductive success should favor a risk-seeking pattern of trait expression, such that male virtue levels show higher variance than female trait values (see Archer & Mehdikhani, 2003). That is, there should be more supervirtuous males but also more virtue-deficient males.

11. Strategic investment in trait based on self-assessed talent: in species such as humans that have several different kinds of behavioral courtship displays, there are different sexual/status niches (Ellis, 2001; Weisfeld, 1999). Juveniles should assess their relative virtues and invest time and

effort in sharpening virtue-display skills preferentially in their highest virtue areas.

Social and Sexual Features

12. *Perceivability*: variation in virtues should be perceivable, directly or indirectly, consciously or unconsciously, by the opposite sex, in a way that could potentially influence mate choice.

13. *Positive correlations with other subjectively desired traits*, such as physical attractiveness, social status, charisma, and so forth; these correlations should be genuine, not just stereotyped “halo effects” (cf. Nisbett & Wilson, 1977).

14. *Positively valued in mate choice*: all else being equal, virtues should be favored in mate choice. Virtues as good-genes indicators may be favored more often by males, in short-term relationships, and by women at peak fertility near ovulation. Virtues as good-parent indicators may be favored more often by females, in long-term relationships, and by women at lower fertility in the cycle. During peak mating effort, virtues may be favored more in the opposite sex than in one’s own sex, and more in potential mates of appropriate age than in younger or older individuals.

15. *Conspicuous courtship display*: during courtship, individuals should conspicuously (if unconsciously) display virtues to the opposite sex. This could be measured across different time scales, comparing courtship to noncourtship situations across ovulation cycle stages, relationship stages, and social contexts.

16. *Young-adult peak in trait expression*: for sexually selected behavioral traits, conspicuous virtue displays should peak in young adulthood, at the peak of mating effort. They should be low before puberty, should increase rapidly thereafter, and should decline gradually as individuals shift their time and energy from courtship to parenting.

17. *Alternative mating strategies*: individuals lacking the sexually attractive virtues should more often pursue alternative mating strategies that try to circumvent mate choice by the opposite sex, including increased use of sexual harassment and sexual coercion (Gangestad & Simpson, 2000; Thornhill & Palmer, 2000).

18. *Positive assortative mating*: in species with social monogamy such as ours, individuals should assortatively mate with respect to virtues, because the competitive mating market should ensure that high-virtue individuals prefer each other, leaving lower virtue individuals no choice but to settle for each other (see Todd & Miller, 1999).

19. Derogation of trait quality in sexual competitors: if virtues are valued in courtship, same-sex rivals should selectively derogate each other with respect to virtue deficits (see Buss & Dedden, 1990).

20. Gossip about trait values: in social species such as ours with collective mate choice that takes into account the views of family and friends, gossip about potential mates should focus some attention on virtues as fitness indicators, with high virtue recognized and praised.

Example: Sexual Fidelity as a Moral Virtue

For example, suppose a researcher hypothesizes that sexual fidelity evolved by sexual selection through mutual mate choice (rather than through kin selection, reciprocal altruism, or group selection). A first step might be to investigate fidelity's sociosexual features. Do surveys, interviews, and experiments show that people prefer sexually faithful mates, all else being equal? Yes: jealousy research shows that men and women across cultures react very negatively to sexual infidelity yet are highly motivated to discover it (Buss, 2000; Shackelford & Buss, 1997). Do people verbally derogate their sexual rivals for being unfaithful, using technical moral-philosophy terms such as "bimbo," "floozy," "skank," "slut," "tart," "tramp," "trollop," "whore" (for females), or "bastard," "bum," "cad," "cheat," "creep," "dog," "knave," "lecher," "rat," "rogue," "scoundrel," "sleazeball," "slimebucket," "snake" (for males). Do people gossip about other people's sexual infidelities, especially to friends and family? (Indeed, if there is an infidelity to gossip about, do we ever gossip about anything else?) Do people conspicuously display their likely future fidelity in courtship, for example, by making impassioned, adaptively self-deceptive declarations of infinite, eternal, exclusive love?

If the answers are generally yes, then the researcher might progress to phenotypic studies of sexual fidelity as an individual-differences dimension. Are there stable individual differences in the likelihood of fidelity versus infidelity, or is infidelity driven entirely by chance and opportunity? Research on the opposite of fidelity, the personality construct of "sociosexuality" (interest in promiscuous, short-term, or extra-pair mating), confirms there are stable individual differences in this trait dimension (Gangestad & Simpson, 2000). Is fidelity positively correlated with other desirable moral virtues and fitness-related traits, such as kindness, conscientiousness, agreeableness, mental health, longevity, and intelligence? (This question becomes complicated, since individuals of higher mate value will be sought more often for short-term, extra-pair copulations, so will be tempted by more opportunities for infidelity—Gangestad &

Simpson, 2000. Mate value and infidelity opportunities would have to be carefully statistically controlled in studies of fidelity's correlations with other moral virtues.)

The genetic studies of infidelity would be the hardest to perform, but often the most informative. Would twin and adoption studies show that the propensity to infidelity versus relationship stability is heritable? (Actually, they do already: Bailey et al., 2000; Cherkas, Oelsner, Mak, Valdes, & Spector, 2004.) Would genetic inbreeding (e.g., offspring of first-cousin matings) reduce fidelity, suggesting a role for partially recessive harmful mutations in driving infidelity? Would one find positive genetic correlations between the tendency to fidelity and the mate preference for fidelity—as might be expected if there has been sexual selection for the trait?

Clearly, the sexual selection hypothesis for moral virtues is eminently testable. However, it requires new ways of thinking about costly signaling adaptations (Miller, 2000b, 2000c). These cannot be assessed using the standard adaptationist criteria for naturally selected traits (e.g., low cost, high efficiency, high modularity, low phenotypic variance, low heritability, and reliable development across all individuals) that are more familiar to evolutionary theorists (e.g., Andrews, Gangestad, & Matthews, 2003; Tooby & Cosmides, 1992). For naturalistic moral philosophy to benefit maximally from contemporary scientific insights, it must not only increase its appreciation of sexual selection's power but also expand its understanding of how to analyze costly signaling adaptations.

Implications for Normative Ethics

Normative ethics is supposed to help us distinguish right from wrong and good from evil. It tries to achieve a “reflective equilibrium” between (1) possible universal moral principles, (2) derived moral implications that would apply in particular situations, and (3) human moral intuitions that react to those principles, implications, and situations (Rawls, 1971; Daniels, 1996). The hope is that normative ethicists can articulate a set of universal, coherent, consistent moral principles that yield intuitively acceptable moral implications across all possible situations and that thereby embody a rational distillation of human moral sensibility. Almost all moral philosophers accept that this is the legitimate goal of normative ethics, though debates still rage between consequentialists and deontologists, between act ethicists and virtue ethicists, and so on. However, if moral virtues arose through sexual selection, this reflective equilibrium approach to normative ethics is likely to fail for at least three reasons.

First, suppose human moral intuitions evolved as part of our person-perception system for inferring stable, morally valenced, mating-relevant personality traits from observable behaviors. If so, we are trying to do ethical alchemy: trying to refine unconscious, domain-specific, species-specific, person-perception adaptations (the base metal) into verbally articulated, domain-general, universal moral principles (the gold). This is likely to be an uphill battle. One reason it is difficult to make our moral intuitions consistent and coherent is that moral intuitions usually precede reasoned moral judgments (Haidt, 2001) and are often driven by morally judgmental emotions that figure prominently in sexual relationships, such as anger (Ellis & Malamuth, 2000), disgust (Rozin, Haidt, & McCauley, 1999), jealousy (Buss, 2000), embarrassment (Keltner & Buswell, 1997), shame (Tangney, 1999), and gratitude (McCullough, Emmons, Kilpatrick, & Larson, 2001).

Second, if our person-perception system relies on social-inference heuristics that are fast, frugal, and pragmatic, then our moral judgments will often violate procedural norms of rationality derived from logic, statistics, and rational choice theory, such as consistency, transitivity, and completeness (Gigerenzer, Todd, & ABC Research Group, 1999). There are deep decision-theoretic reasons why it may be impossible to derive a set of consistent, coherent moral preferences from the operation of such social-inference heuristics. To know whether this is a fatal objection to the reflective equilibrium approach to normative ethics, we need to learn a lot more about moral judgment heuristics in the context of person-perception research (e.g., Funder, 2004; Haselton & Funder, *in press*).

Third, human moral intuitions evolved to assess people's stable moral virtues in ancestrally typical, fitness-relevant situations, and to guide ancestrally feasible forms of social response such as forming friendships or mateships, gossiping about liars, punishing cheaters, or ostracizing psychopaths. There is no reason to expect our moral intuitions to show consistent, logically defensible reactions to evolutionarily novel moral dilemmas that involve isolated, hypothetical, behavioral acts by unknown strangers who cannot be rewarded or punished through any normal social primate channels.

For example, we often seem cognitively paralyzed by many current debates in reproductive bioethics (Petrinovich, 1995). How should we feel about abortion, sperm donation, egg donation, surrogate pregnancy, human cloning, genetic testing, or genetic enhancement? Different framings of these issues will activate different, domain-specific moral intuitions (Haidt, 2001). This is precisely why rhetorical metaphors are effective in

such moral debates. For example, “genetic enhancement” may seem pernicious fascism if we view it as a limited resource that will be appropriated by the powerful for their nefarious ends, or it may seem democratically liberating if we view it as a natural extension of good-genes mate choice, for those whose own suboptimal mate value precludes getting good genes from a willing partner (Miller, 2000a). Is there any neutral, rational position from which we can judge such issues, without assimilating them to one or another of our domain-specific moral intuitions? Probably not: rational decision making depends upon subjective utility functions that must be supplied either by the genetic imitation of ancestral utilities (“gut instinct”) or the social imitation of peer utilities (“learning,” “social norms”). Gut moral instincts will be mute or misleading guides to moral dilemmas raised by new technology, and moral conformity to peer opinion will be biased by vested political, corporate, and media interests that define the current “ethical issues” in their own interests.

These three evolutionary psychology problems resemble some philosophical problems with the reflective equilibrium method (Brandt, 1990). Basically, there is no compelling logical reason to think that our moral intuitions have any true normative credibility as guides to genuinely moral behavior, and a coherently systematized set of these subjective moral fictions will remain fictional. Of course, there may be evolutionary reasons to expect that species-typical human moral intuitions would tend to maximize inclusive fitness under ancestral conditions. However, that is quite different from claiming that they are normatively justifiable in any broader sense. For example, Peter Singer (1990, 1994) has made some compelling but counterintuitive arguments concerning animals rights, euthanasia, and infanticide; in such cases, it seems impossible to reach a reflective equilibrium between our gut moral instincts and our scientifically informed normative judgments.

In the light of these moral-psychological problems, consider two different forms of a typical normative-ethics question. Abstract form: Is it morally right to assassinate a genocidal war criminal? (Perhaps—many have praised the attempted assassination of Adolf Hitler by Colonel Claus von Stauffenberg on July 20, 1944). Personal form: Suppose there is a twenty-first-century head of state who ordered his country into a fraudulent and illegal war that resulted in thousands of needless civilian casualties, but who is almost certain to avoid accountability to the International Criminal Court in The Hague. Would it be moral to feel sexually attracted to a man who succeeded in killing the wicked head of state, with a single head shot from a Barrett M82A1 .50-caliber semi-automatic sniper rifle at 800 meters

on a windy day? The personal form is much more specific about the identities of the moral judgment maker, the morally judged individual, the civilian victims, the nature of the assassination, and the fitness-relevant, sociosexual implications of the moral judgment. These details should and do matter in making adaptive mate-choice judgments about the moral virtues of snipers. A woman who knows her ordnance might admire the sniper's good-genes indicators, such as his resourcefulness (the M82A1 costs \$7,775 retail), his physical condition (the rifle is 5 feet long and weighs 34 pounds), and his marksmanship (the 800-meter head shot was near the rifle's maximum effective antipersonnel range of 1,000 meters). Yet she may equally worry about his good-dad indicators: his vigilante action may reveal psychopathy, paranoid schizophrenia, bipolar disorder, impulsiveness, fame-seeking narcissism, or high-risk sensation seeking (Fein & Vossekuil, 1999; Meloy, James, Farnham, Mullen, Pathe, Darnley, & Preston, 2004). She can only tell by gathering further information about his virtues, both moral and nonmoral—which is the function of prolonged human courtship.

Note

For helpful discussions, guidance, and/or feedback on these ideas, thanks to Paul Andrews, Rosalind Arden, Helena Cronin, Oliver Curry, Dylan Evans, Steve Gangestad, Walter Sinnott-Armstrong, and Peter Todd.

4.1

Why Moral Virtues Are Probably Not Sexual Adaptations

Catherine Driscoll

*For a short time he loved me sincere, he used me both kindly and civil
The honeymoon scarcely was o'er, when he turned out a quare divil!*

—Trad.

Geoffrey Miller's work in evolutionary psychology is nearly unique in its emphasis on the importance of Darwin's "other theory"—sexual selection—in human evolutionary history. It's an important reminder not to neglect this possible explanation for human physiological and psychological traits and, as such, is a very interesting and useful contribution to the study of "human nature." However, I doubt that Miller's explanation for moral virtues as involving a combination of sexual selection and group selection will work.

Sexual selection theory claims that the presence or fixation in a population of some trait of organisms of one sex can sometimes be explained in terms of the sexual choices of members of the opposite sex, or by sexual competition, and not because of the contribution that trait plays in the survival of the individual that possesses it. A classic example of such a trait is the peacock's tail. The showy tail contributes nothing to the survival of the peacock; if anything, the tail is actively detrimental, since it increases the peacock's risk of being killed by predators. What the peacock's tail does do is make the peacock more attractive to peahens. Peacocks with big showy tails attract more mates than peacocks without, and hence they have more offspring with tails like their own. The biggest problem that sexual selection theory faces is that peahens, and their preferences, are also subject to natural selection. Peacocks without big showy tails are fitter than peacocks with such tails, all else being equal; only peahens' choices make the difference. Thus, peahens who make choices of mates who are otherwise fitter ought to do better than those who make choices of mates who are less fit, because good choosers have fitter offspring and thus ultimately

more grandchildren than bad choosers. Therefore, sexual selection theory needs some way of explaining why peahens that like showy tails have not become selected against in favor of more sensible peahens. The suggested solution to this problem (Zahavi & Zahavi, 1997) is that costly traits like peacocks' tails act as signals of the fitness of their bearers. Choosing a fit mate is a difficult decision/problem for a peahen—she cannot determine, by ordinary observation, which peacock is the fittest. What peahens need is a reliable way of telling when peacocks are fit and when they are not. The proposal made is that complex showy traits like peacocks' tails work as indicators of the overall fitness of the peacock. By choosing good tails, the females choose mates who are fitter overall. The idea is that peacock tails can only be made by peacocks that have other sorts of good genes and hence can “afford” the fitness cost of a fancy tail. This works so long as good tails are well correlated with good genes, which means choosing good tails allows females to reliably choose good genes. This solves the problem of the evolution of mate preferences. Since there is no other way to choose highly fit mates, fancy tail preferences win over non-fancy-tail preferences.

This problem of the origin of mate preferences is one that surfaces again in Miller's work. Miller's paper does not claim that the virtues came about in *exactly* the same way as the peacock's tail—that is, because they acted as a costly signal. Instead, moral virtues are supposed to spread via a combination of sexual selection and group selection. Miller's claim is that the moral virtues spread primarily via group selection, but that getting group selection going required something to break the nonmoral equilibrium that existed in groups before morality arose. Group selection occurs when groups differ in their group-level properties rather than in the properties that belong to the individuals that make up those groups, and that because of differences in group-level properties, some groups give rise to more new groups than others. An example of a group-level property would be “composed largely of virtuous individuals”; an example of an individual-level property would be “possessed of moral virtues.” Moral virtues could spread via group selection if groups with larger numbers of individuals with virtues gave rise to more new groups than groups without. This requires, however, that there be groups which are composed largely of virtuous individuals. The problem is that while moral individuals are assumed to do well in all moral groups (since, e.g., moral individuals avoid punishment that might be given to nonmoral individuals), they tend to do poorly in all nonmoral groups (since they're exploited by nonmoral individuals or are not as ruthless in pursuit of their interests as nonmoral individuals).

This means that while groups with many moral individuals would be selected for once they existed, it would be hard to get large numbers of moral individuals in groups to start with, since moral individuals are selected against when they arise. Miller is suggesting that mate preferences for moral virtues could solve this problem—mate preferences for virtues would lead to individuals with virtues having greater numbers of offspring, and this would lead to an increase in the numbers of moral individuals within groups, breaking the nonmoral equilibrium. Once the numbers are high enough, group selection for the highly moral groups could get going.

This is an interesting idea, but it creates a problem—how do mate preferences for moral individuals evolve if moral individuals were less fit than those without morals? I presume we're assuming that preferences for virtues are competing with neutral mate preferences, and both exist in these groups. However, if this is the case, then neutral preferences will evolve at the expense of preferences for virtues. If individuals with moral virtues are less fit, then their (moral) offspring are less fit, and thus the offspring of those that mate with them. Hence, individuals with moral mate preferences would get selected against within groups, just as would moral individuals themselves. So why would preferences for moral mates arise? One possibility is that moral virtues are a costly signal, like the peacock's tail. Mate preferences for moral virtues persist because by choosing moral virtues, individuals choose mates who are overall fitter. Thus, despite the fitness cost that moral virtues impose on their possessors, preferences for moral virtues could evolve. In other words, moral virtues act as costly signals or fitness indicators, just like the peacock's tail.

So could moral virtues be costly signals? The case of the peacock's tail allows us to identify six important characteristics that costly signals need to have. First, and most obviously, costly signals need to be demonstrably costly. They need to have a negative fitness effect that can only be managed by an individual with plenty of fitness "to spare." Second, they need to be employed in sexual choice—individuals actually have to use the trait that acts as a signal as a means of choosing between partners. Third, they need to be heritable, such that parents with the costly signal trait have offspring with that trait. Fourth, the costly signal trait has to correlate well with some reasonable fitness-increasing trait or traits. Fifth, the signal has to be hard to fake—that is, it mustn't be possible for individuals to routinely deceive others into thinking that they have that trait; otherwise individuals with preferences for the signal will not reliably choose better mates and that preference will be selected against. Finally, preferences for costly

signals are only selected for in cases in which the information the costly signal provides cannot be more easily acquired in some other way. So how does Miller do at showing that these six things are true of moral virtues?

I think Miller's evidence for the first through fourth characteristics (i.e., costliness, use in courtship, heritability, and correlation with other fitness-increasing traits), though sometimes anecdotal, is not highly problematic; he has a tendency to construe "virtue" and "vice" rather loosely to compensate for the absence of discussion in the psychology and biology literature of the traits that *philosophers* might think of as virtues, but this is not his fault. There are much more serious problems, however, with how far the fifth and sixth characteristics of costly signals apply to moral virtues. Preferences for costly signals only evolve in a context in which the costly signal can't be faked *and* when there isn't any other reliable but less costly way for the one relying on the signal to acquire the information it conveys. This raises two problems for moral virtues as costly signals. The first is that courtship for humans usually isn't all that long a period of time, and it is in the interests of individuals without virtues to temporarily pretend to be virtuous—to be kind to the stepchildren, to be generous to the waitstaff on dates—in order to secure sexual access to the other person. It might also be possible to fake good behavior for longer periods of time by being good when observed, saying the right things, and so forth, to secure one's social and sexual relationships, while at the same time using every opportunity to exploit others and behave immorally. Both of these strategies are relatively cheap (and anecdotally widely recognized) ways of exploiting the mate preferences of other individuals without paying the cost of really being moral, and they would undermine the selection in favor of preferences for moral virtues. Hence, moral virtues don't look like reliable, unfakeable costly signals.

The second problem is that Miller has not demonstrated that moral virtues provide information about the fitness of their possessors that can't be acquired any other (cheaper) way. Miller claims that moral virtues signal a low mutation load in a person's genes. The idea is that the brain systems that produce morality are complicated and require lots of genes to build them, to the extent that even a few mutations could quickly end a person's capacity to be moral. Hence, an individual could tell that potential partners are free of mutations if they behave morally. However, Miller doesn't provide any evidence that only people with generally undamaged brains can manage moral virtues. Indeed, I might note that individuals with

certain severe genetic or developmental syndromes such as Down's or Williams syndrome might be considered more virtuous in some regards than many normal individuals—they are noted for their kindness, friendliness, and sociability. However, they are often severely mentally disabled. Instead of trying to offer evidence for the general claim that moral virtues signal good genes, Miller tries to show that moral virtues are correlated with particular fitness-increasing traits such as general intelligence. This leaves him with a new problem—costly signaling isn't needed to choose mates with the traits Miller discusses. It is as easy to see if your mate is smart, for example, as to see if he or she is generous or kind—by seeing how well he or she handles language, say, or crossword puzzles, or solves more serious problems. These other abilities involve little or no fitness cost (or even a fitness benefit) to their bearer. If an individual can make judgments of a potential partner's intelligence using such abilities, why rely on whether they have moral characteristics? Choosing a mate with a costly signal trait leads an individual to have offspring with the costly signal trait and hence ultimately represents a fitness cost to that individual.

If Miller wants to show that moral virtues are a costly signal, he needs to show either that moral virtues can only be present in generally good brains or that there is a correlation between virtues and fitness-increasing traits that cannot be observed directly. However, he has not done either of these things. This strongly suggests there is a serious problem with the explanation Miller is offering. However, some of Miller's evidence is, at the very least, intuitively compelling. If moral virtues have not arisen by sexual selection, then why are we so interested in moral virtues in our partners? My worry is that there are two perfectly reasonable alternative stories that explain our preferences without purporting to explain the origin of moral virtues. The first is that our preferences for moral individuals evolved (culturally or genetically) because being moral was itself an advantage in all-moral groups in which there was punishment or other forms of exclusion for those who were nonmoral. It was important for one's children to be moral, and hence mating with moral people was fitness increasing. Hence mate preferences for moral virtues were another way for individuals in moral groups to ensure their and their children's reproductive success. In other words, once morality was established by other means, it became worthwhile to prefer moral people as sexual partners. Space prohibits me from exploring some of the suggestions for how tendencies for morality might have evolved, but there are plenty of alternatives, primarily some

form of explanation involving cultural or genetic group selection (e.g., Henrich & Boyd, 1998; Sober & Wilson, 1998). The second story, and perhaps one that is even more likely, is that preferences for moral mates involve simple self-interest—no one wants to marry a nasty person, since nasty people tend to be nasty to you and hurt you and your children or make you unhappy. Mate preferences for moral individuals could simply involve the use of more ordinary general preferences for safety and well-being and, thus, wouldn't need a separate explanation in terms of sexual selection theory.

Oliver Curry

There has been a long-standing debate in the history of moral thought over the nature of virtue—the enduring traits that are indicative of a good moral character. One tradition—represented by Aristotle, Cicero, Machiavelli, Nietzsche, and Hume—has celebrated the so-called “pagan” virtues of beauty, strength, courage, magnanimity, and leadership. Another tradition—represented particularly by theologians—has celebrated exactly the opposite set of traits: the so-called “Christian” virtues of humility, meekness, quietude, asceticism, and obedience (Berlin, 1997). But what are the virtues? Where do they come from? Why do they consist of these two apparently incompatible sets of traits? And why have they been considered moral?

Geoffrey Miller rightly argues that the virtues are not explained by existing evolutionary theories of morality, such as kin or reciprocal altruism. Instead, Miller argues, such traits are the product of sexual selection; specifically, they are products of mate choice for reliable signals of genetic and phenotypic quality. Thus, the virtues are analogous to the peacock’s tail; they are dazzling, conspicuous displays of the qualities and character traits that members of the opposite sex look for in a mate.

However, Miller’s theory leaves two kinds of virtues unaccounted for: first, virtues displayed in contexts other than courtship and, second, the traditional Christian virtues. Moreover, Miller’s theory doesn’t explain why some sexually attractive traits—such as beauty—have been considered moral. Nor does it provide a criterion for distinguishing sexually attractive traits that are morally virtuous, such as beauty, from sexually attractive traits that are morally neutral, such as immuno-compatibility.

I shall outline a more comprehensive evolutionary theory of virtue. This “conflict-resolution theory” argues that the virtues are adaptations for competing without coming to blows; they serve to avoid, forestall, or defuse more violent means of competing for scarce resources. This theory

incorporates both the “pagan” and the “Christian” virtues. The pagan virtues are “signals of superiority.” They are used to resolve conflict in two ways. First, they are used to attract mates—for here, natural selection has favored aesthetic and altruistic displays over aggression as a means of competing for mates. These are the virtues that Miller draws attention to. Second, signals of superiority are used to deter rivals. They do this as part of a “display-defer” strategy—that is, a strategy that uses, on the one hand, displays of fighting prowess and, on the other hand, ritual displays of deference to superior displays to turn otherwise bloody battles into relatively harmless contests. These displays of prowess are the second kind of pagan virtue. And this brings us to the Christian virtues. For they are the flip side of the display-defer strategy of resolving conflicts. They are “signals of submission,” conspicuous displays of deference that bring conflict to an end.

Thus, the conflict-resolution theory provides a secure theoretical foundation that accounts for a broader range of virtues and that subsumes Miller’s mate-choice theory. What is more, the conflict-resolution theory explains why these particular sets of traits have been seen as moral; it is because, like other aspects of morality, they constitute a successful solution to one of the recurrent problems of social life—in this case, the problem of settling disputes.

Below I briefly review the evolutionary theory of conflict resolution and look at some animal examples. I review the evidence for equivalent traits in humans. And I show how the conflict-resolution theory of virtue makes sense of various aspects of traditional moral thought.

The Virtues of the Hawk and the Virtues of the Dove

The conflict-resolution theory of virtue begins with the logic of animal conflict. Animals often come into conflict over resources such as food, territory, and mates. On the surface, such conflicts look like straightforward zero-sum games. However, in fact, there are costs involved in conflict—time, energy, and injury—that the players have a common interest in avoiding. For this reason, in the paper that first introduced evolutionary game theory, John Maynard Smith and George Price (1973) portrayed animal conflict as a nonzero-sum game—specifically, a hawk-dove game in which the worst outcome occurs if both players adopt a “hawkish” strategy of all-out aggression. Thus, conflict presents combatants with an opportunity to cooperate, in the sense of competing in less mutually destructive ways.

Over evolutionary time, natural selection has favored a number of ways of competing that involve an exchange of signals rather than an exchange of blows. These signals provide reliable information about the relative merits of the protagonists—be it genetic or phenotypic quality, or formidability—that can settle the dispute without resort to violence. It is the traits that convey this information that have been called “virtues”.

The pagan virtues—beauty, strength, courage, magnanimity, and leadership—are “signals of superiority.”

Consider beauty. Many animals, when competing for mates, eschew violence and instead devote their energies to spectacular aesthetic displays. Peacocks, for example, compete for mates not by fighting but by growing beautiful tails. These tails act as reliable indicators of the birds’ genetic and phenotypic quality, allowing a peahen to make a judicious choice from among her eager suitors, rather than having them fight it out among themselves. In other species, bright coloration, symmetrical plumage, singing, dancing, and creativity perform a similar function (Cronin, 1992; Darwin, 1871; Miller 2000; Ridley, 1993).

Now consider strength, or “fortitude.” When engaged in direct competition with other individuals—over food, territory, and mates—many animals avoid all-out war by employing a strategy that combines “hawkish” displays of prowess with “dove-ish” displays of deference to superior displays. Maynard Smith and Price showed that such a strategy is evolutionarily stable because, when combatants differ in their ability to win a fight, it pays both parties to establish who is likely to prevail by means of an exchange of signals that reliably indicate each party’s fight-winning abilities rather than through a violent battle. And, once established, it pays the weaker party to bow out gracefully. This way, the stronger wins the resource he was going to win anyway, and both parties benefit by avoiding the costs of conflict (Clutton-Brock & Albon, 1979).

The classic example of this “display-defer” strategy comes from a study of stag red deer competing over the control of harems. The contest begins with a roaring match lasting several minutes. Roaring is a reliable signal of size and strength; usually, the stag with the less impressive roar will retreat. However, if the stags are too closely matched for their roars to be decisive, the contest moves to a “parallel walk” stage, where the combatants have the chance to size one another up. If this doesn’t settle the dispute, then the stags lock antlers and begin a pushing contest, and the loser retreats. In other competitions in other species, hawkish displays of size, weight, age, and experience may carry the day. (For a review, see Riechert, 1998.)

Next, consider altruism. Some creatures settle disputes by means of displays that, as an added bonus, provide benefits for their audience. Male ravens, for example, compete for mates not by fighting but by performing “acts of bravery”; they undertake the risky task of checking to see whether potential carrion is in fact dead and not merely sleeping or injured. “[B]y demonstrating that they have the courage, experience, and quickness of reaction to deal with life’s dangers,” says Frans de Waal (1996, 134), “the occasional boldness of corvids serves to enhance status and impress potential mates.” Similarly, male chimpanzees sometimes compete through “magnanimity”—that is, altruism directed to subordinates. They take risks in order to provide the troop with food, are generous with their own kills, and confiscate the kills of others and redistribute them. As de Waal observes, “instead of dominants standing out because of what they take, they now affirm their position by what they give” (1996, 144). Also, some primates compete for status through “public service” or “leadership”—that is, altruism in support of other forms of cooperation. Thus, dominant chimpanzees, stump-tailed monkeys, and gorillas all compete by intervening to end disputes among subordinates (Das, 2000; de Waal, 1996). These dominant individuals are unusual in that they intervene not in support of their families and allies but “on the basis of how best to restore peace” (de Waal, 1996, 129). Consequently, “the group looks for the most effective arbitrator in its midst, then throws its weight behind this individual to give him a broad base of support for guaranteeing peace and order” (de Waal, 1996, 130).

Thus, beauty, strength, courage, magnanimity, and leadership are all examples of traits that provide reliable information about the underlying qualities of the protagonists. They serve to attract mates or deter rivals. And, by doing so, they reduce or avoid the costs of violent conflict. In this way, evolutionary theory explains the existence, and conspicuous display, of exactly those hawkish traits that, in humans, have been called the “pagan virtues.”

But what about the apparently opposite set of Christian virtues—humility, meekness, quietude, asceticism, and obedience? Conflict-resolution theory has a ready explanation for these, too. They are “signals of submission,” the conspicuous displays of deference that form the flip side of the display-defer strategy of resolving conflicts. They manifest the “dove-ish” branch of the strategy—recognizing when you’re beaten and signaling to your opponent that you accept defeat and intend to withdraw, thereby bringing the conflict to an end.

Not surprisingly, dove-ish cues of submission have been designed by natural selection to be the exact opposite of hawkish cues of dominance.

Indeed, cues of submission were Darwin's prime example of "the principle of antithesis" in the expression of emotions: "directly opposite state[s] of mind" lead to "the performance of movements of a directly opposite nature" (Darwin, 1872/1998, 55). For example, when discussing submission in dogs, Darwin observed that:

The feeling of affection of a dog towards his master is combined with a strong sense of submission, which is akin to fear. Hence dogs not only lower their bodies and crouch a little as they approach their masters, but sometimes throw themselves on the ground with their bellies upwards. This is a movement as completely opposite as is possible to any show of resistance. . . . By this action [the dog seems] to say more plainly than by words, 'Behold, I am your slave.'¹

In social species, where regular contests lead to the formation of hierarchies, displays of submission become swifter and more symbolic—they involve elaborate greeting rituals or "etiquette." For example, subordinate macaques give a "silent bared-teeth display" and chimpanzees "use a vocal-gestural signal of subordination consisting of repetitive pant-grunting and bowing towards the dominant."²

Thus, traits such as humility, meekness, quietude, asceticism, and obedience can be seen as different manifestations of submission—of the tendency to beat a strategic retreat in the face of overwhelming odds—which is an integral part of the display-defer strategy of resolving disputes. In this way, evolutionary theory explains the existence, and conspicuous display, of exactly those dove-ish traits that, in humans, have been called the "Christian virtues".

Thus the conflict-resolution theory explains the origin of hawkish "pagan" and dove-ish "Christian" virtues. And it also explains why these traits have been considered moral. It is simply because, like other aspects of morality, the virtues solve a recurrent problem of social life, to the benefit of all those involved. Just as conventions solve coordination problems, and reciprocity solves free-rider problems, virtues solve conflict-resolution problems.

Human Adaptations for Conflict Resolution

Let's now turn to our own species. Given how widespread adaptations for conflict resolution are in nature, especially among social primates, and given that there is no reason to suppose that such traits have been erased during the course of hominid evolution, we should expect to find an equivalent set of adaptations in humans. And indeed we do.

This aspect of human nature was first described and documented by that perceptive student of the human condition, David Hume. Indeed, his account of virtue strikingly anticipates many aspects of the conflict-resolution theory that I have outlined.

David Hume compared human virtue to the hawkish displays of “excellence”—such as the peacock’s tail and the nightingale’s song—exhibited by other animals. He argued that “the same qualities cause pride in the animal as in the human kind; and it is on beauty, strength, swiftness or some other useful or agreeable quality that this passion is always founded” (1739/1985, 376–7). Hume proceeded to argue that pride is “essential to the character of a man of honour,” and that it gives rise to traits that benefit others—the “heroic” or “shining virtues” of “[c]ourage, intrepidity, ambition, love of glory, magnanimity” (1739/1985, 376–7).

Hume also discussed the social utility of dove-ish traits, such as humility. He notes that differences in ability give rise to hierarchies in which “certain deferences and mutual submissions” are required “of the different ranks of men towards each other.” He says, “Tis necessary, therefore, to know our rank and station in the world, . . . to feel the sentiment and passion of pride in conformity to it, and to regulate our actions accordingly.”³ Humility, or “a just sense of our weakness,” then “is esteem’d virtuous, and procures the good-will of everyone” (Hume 1739/1985, 642).

Hume even explained why dove-ish virtues have become associated with the Christian church. He argued that humility, combined with contemplation of a “supreme being,” tends to produce exaggerated submission displays. The thought of an omnipotent god, fostered by religions such as Christianity, is apt “to sink the human mind into the lowest submission and abasement, and to represent the monkish virtues of mortification, penance, humility, and passive suffering, as the only qualities which are acceptable to him” (Hume 1757/1889, 43). In such circumstances, says Hume, “instead of the destruction of monsters, the subduing of tyrants, the defence of our native country; whipping and fasting, cowardice and humility, abject submission and slavish obedience, are become the means of obtaining celestial honors among mankind.”⁴

Hume managed to get this far without the aid of modern evolutionary theory. We now have the theoretical and empirical tools to develop a more up-to-date account of human virtue. And, already, several strands of research are providing support for the hypothesis that humans possess adaptations for conflict resolution, and they are beginning to shed light on exactly what they look like.

First, Allan Mazur and Alan Booth (1998) have documented how, in humans as in other animals, the hormone testosterone regulates participation in dominance encounters. Testosterone rises in anticipation of a challenge, thereby boosting “coordination, cognitive performance, and concentration” (Mazur & Booth, 1998). After the contest, levels of testosterone remain high in the winner—he experiences “increased assertiveness, and a display of dominant signs such as erect posture, sauntering or striding gait, and direct eye contact with others. [He] may seek out new dominance encounters and [is] bolstered to win them.” The loser, meanwhile, experiences a drop in testosterone “reducing his assertiveness, diminishing his propensity to display the dominant actions associated with high status, and increasing his display of such submissive signs as stooped posture, smiling, or eye aversion. . . . Faced with a new dominance encounter, [the loser] is more likely than before to retreat or submit” (Mazur & Booth, 1998, 359).

Second, there is evidence that, in addition to displays of physical prowess, men signal status with displays of intelligence, aestheticism, and creativity—the human equivalent of the peacock’s tail or the nightingale’s song. As Geoffrey Miller (2000a) has observed, in every cultural sphere, including art, music, and literature, men are responsible for around ten times as much cultural production as women; male cultural production peaks at the same time that testosterone and mating effort peaks (i.e., during early adulthood); and displays of intelligence, wit, and creativity form an important part of human courtship.

Third, there is anthropological evidence that men compete for status by performing acts of generosity and largesse, in the form of potlatch feasts, bonanzas, and festivals. For example, Kristen Hawkes et al. argue that Hazda hunters compete for status and access to mates by means of big-game hunting, which can be seen as a form of “showing off” (Hawkes, 2001). This form of hunting generates more food than a hunter or his family can eat, and the surplus meat is not distributed in the expectation of reciprocity. Rather, the distribution of meat from the kill serves to raise the hunter’s status among other men and to increase his access to mates. Hawkes reports that successful hunters are more often named as lovers and have more surviving offspring. Selection of such altruistic signals is consistent with the observation that “generosity” is universally admired in leaders (Brown 1991, 137–140).

Fourth, as predicted, women find “winning” cues of dominance and status sexually attractive (Buss, 1994; Ellis, 1992; Miller, 1998). As the anthropologist Edgar Gregersen concludes from a study of almost 300

cultures: “for women the world over, male attractiveness is bound up with social status, or skills, strength, bravery, prowess, and similar qualities” (Gregerson, 1982). Not surprisingly, high-testosterone males also report more sexual partners (Townsend, 1998). The conflict-resolution theory of virtue also predicts that, in the context of male-male competition, men should attend to, be intimidated by, and defer to hawkish traits in other males. Unfortunately, perhaps because the answer seems so obvious, this prediction has yet to be rigorously tested.

Finally, humans display typical mammalian cues of submission. As the ethologist Desmond Morris observes:

Passive submission in the human animal is much the same as in other mammals. In extreme cases it takes the form of cringing, crouching, grovelling, whimpering, and attempts to protect the most vulnerable parts of the body. . . . It presents a picture of “instant defeat” and thereby avoids the damaging physical process of actually being defeated. Its success depends on the presentation of signals which are the exact opposite of the threat signals of our species. A threatening man will square up to an opponent, his body tense, his chest expanded, his face glaring, his fists clenched, his voice deep and snarling. By contrast, the submissive individual tries to make his body seem as small and limp as possible, with shoulders hunched, his face wincing, his hands spread, and his voice high and whining. (1982, 217)

More symbolic versions of these signals—in the form of greetings, manners, etiquette, and other marks of respect—are used to lubricate formal dominance hierarchies (Morris, 1982, 217–228). And, intriguingly, the tendency to ignore cues of submission in an opponent—and hence to continue attacking a defeated foe—is one symptom of psychopathy (Blair 1997).

Much work remains to be done to develop and test this theory of human adaptations for conflict resolution. However, it is reasonable to conclude that humans do indeed possess such adaptations. We can also be confident that further attempts “to introduce the experimental method of reasoning into moral subjects” will, as Hume envisaged, shed yet more light on the nature of the virtues.⁵

Traditional Accounts of the Virtues

The conflict-resolution account of virtue provides a rich deductive structure in which to locate, make sense of, and reconcile several previous theories of, and observations about, the virtues.

First, the conflict-resolution theory neatly reconciles the “pagan” and “Christian” accounts of virtue. In the absence of such a theory, the celebra-

tion of two diametrically opposed sets of moral virtues has been something of a scandal for moral philosophy. Surveying the debate between the pagans and the Christians, Isaiah Berlin (1997) concluded, rather gloomily, that the two sets of virtues are “incompatible” and “incommensurable”; that there is no prospect of reconciling them; and that this undermines the philosophical project of finding the single best way to live. However, as we have seen, it is a prediction of, rather than a problem for, the conflict-resolution theory of virtue that there should be two sets of traits—the virtues of the hawk and of the dove—and that these two sets should appear to be opposites. Contrary to Berlin, the theory shows that these sets of virtues are neither “incompatible” nor “incommensurable.” On the contrary, they are two sides of the same coin—two aspects of the same component of human nature. They are complementary in that they work together to keep the peace, and their contribution can be measured in the common metric of cooperation.

Second, the conflict-resolution theory explains a wide range of miscellaneous observations about virtue. For example, it explains why the word “virtue” comes from the Latin for “proper to a man” (as in “virile”);⁶ why Aristotle argued that the most virtuous man will “offer aid readily” but “is ashamed to accept a good turn, because the former marks a man as superior, the latter as inferior” (Aristotle 1962, IV, iii, 246); and why Nietzsche argued that virtues reveal “processes of physiological prosperity or failure” and exhibit “the charm of rareness, inimitableness, exceptionalness, and unaverageness” (quoted in Miller 2000a, 337–338). The conflict-resolution theory also accounts for “superogatory acts”—acts of benevolence, mercy, heroism, and self-sacrifice that are “beyond the call of duty”—whose explanation eluded John Rawls.⁷ The theory explains why Hume, Machiavelli, and Nietzsche criticize the Christian church for inculcating extreme “monkish” virtue—a “slave morality”—at the expense of more socially useful “heroic” virtue. And the theory explains why males and females have, traditionally, had different virtues; why the traits used to compete for paternal investment—beauty, chastity, and fidelity—are among the traditional “feminine virtues”; and why it is possible for men, but not women, to regain their “virtue” once it has been lost.

Conclusion

In recent years, evolutionary psychologists have begun to chart the evolved mechanisms responsible for moral thought and behaviour. Kin selection explains family values and the prohibition against incest; mutualism

explains sympathy, friendship, and convention; and reciprocal altruism explains trust, gratitude, guilt, and punishment.⁸ To this list we may now add: conflict resolution explains virtue.

The theory of conflict resolution explains why humans and other animals engage in displays of prowess and why they defer to superior displays. It explains how these hawkish and dove-ish traits help to solve a recurrent problem of cooperation—the problem of conflict resolution. And it explains why two apparently incompatible sets of traits have been celebrated as moral virtues.

Geoffrey Miller has led the way in one area of this theory. He has used evolutionary theory to derive predictions about the form and function of the signals employed in mate choice, and he has outlined a promising program of research that puts the predictions to the test. What we now need are parallel research programs in the other areas of conflict-resolution theory—answering in more detail such questions as the following: How does the psychology of dominance and submission work in humans? Which “virtues” are most effective in commanding deference and respect? To what extent are the virtues heritable? What age and sex differences do they exhibit? Which aspects of the environment are important for the development of the virtues?

Progress in this area will see a further branch of human morality demystified and its study placed on a firm scientific basis.

Notes

I should like to express my gratitude to Helena Cronin for her invaluable support and assistance at every stage of writing this commentary.

1. Darwin (1872/1998, p. 120). The same applies to submission cues in other species. As the primatologists Preuschoft and van Schaik (2000) put it: “While threat displays accentuate size and weapons and elicit yielding on the part of the recipient, displays of submission reduce apparent size, conceal weapons, and correlate with yielding on the part of the sender” (p. 85).
2. Preuschoft and van Schaik (2000, p. 93, p. 96). Established hierarchies constitute a further de-escalation of hostilities. To quote Preuschoft and van Schaik, “dominance in groups seems to function as a conflict management device, preventing escalated competition by conventionalizing means and priority of access [to scarce resources], thus allowing for peaceful coexistence of group members” (p. 90).
3. Hume (1739/1985, p. 650). “A sense of superiority in another breeds in all men an inclination to keep themselves at a distance from him, and determines them to

redouble the marks of respect and reverence, when they are oblig'd to approach him" (p. 441).

4. Hume (1757/1889, p. 43). Desmond Morris (1982) concurs:

Religious Displays . . . are submissive acts performed towards dominant individuals called gods. The acts themselves include various forms of body-lowering, such as kneeling, bowing, kowtowing, salaaming and prostration; also chanting and rituals of debasement and sacrifice; the offering of gifts to the gods and the making of symbolic gestures of allegiance. The function of all these actions is to appease the super-dominant beings and thereby obtain favours or avoid punishments. . . . Subordinates throughout the animal world subject themselves in a similar way. But the strange feature of these human submissive actions is that they are performed towards a dominant figure, or figures, who are never present in person. (p. 229)

5. "An Attempt to Introduce the Experimental Method of Reasoning into Moral Subjects" is the subtitle to Hume's *A Treatise of Human Nature*.

6. "Appelata est enim a viro virtus: viri autem propria maxime est fortitudo" ("The term virtue is from the word that signifies man; a man's chief quality is fortitude"; Cicero, 1945, I, ix, 18).

7. "It is good to do these actions but it is not one's duty or obligation. Supererogatory acts are not required, though normally they would be were it not for the loss or risk involved for the agent himself. . . . Supererogatory acts raise questions of first importance for ethical theory. For example, it seems offhand that classical utilitarian theory cannot account for them" (Rawls, 1971, p. 117).

8. For example, see Cosmides and Tooby (2005a); Lieberman, Tooby, and Cosmides (2003); Tooby and Cosmides (1996); Trivers (1971).

Geoffrey Miller

Catherine Driscoll and Oliver Curry provided thoughtful commentaries that suggest some refinements of my theory and some new directions for research. For clarity, I'll enumerate my responses.

First, my chapter relies heavily on costly signaling theory and sexual selection theory to explain moral virtues, as reliable indicators of general fitness that were favored in mate choice. Catherine Driscoll is correct that any costly signaling explanation for a trait must ideally show that the most attractive form of the trait is hard to fake, and she argues that moral virtues would have been rather easy to fake in prehistoric courtship. If this were true, my theory would not work. However, I think she underestimates what our Pleistocene ancestors could have learned about each other's moral virtues before having sex long enough to get pregnant. As I argued in *The Mating Mind*, prehistoric courtship would have occurred in a highly social context of small hunter-gatherer groups, in which everyone knows everyone pretty well—either personally or by reputation. Courtship would not have been like strangers meeting privately in a single's bar. Any budding sexual relationship would have provoked active information gathering, incisive judgment, and vociferous commentary by all interested parties, including both lovers' friends and families. This is standard procedure in all traditional cultures, from !Kung san hunter-gatherers through Jane Austen's Regency England.

Gossip, reputation damage, and social ostracism are potent deterrents—not just to free riding in reciprocal altruism but also to misbehaving in any way that undermines one's chances of mating well. Sexual gossip—especially gossip about the moral faults of would-be seducers—is especially salient, memorable, and quick to spread (Foster, 2004; West & Salovey, 2004). This is why psychopathy never evolved even a 1% prevalence in traditional societies. The sexually exploitative, seduce-and-abandon psychopaths who thrived in the last few hundred years of chaotically

migratory European colonialism would have been quickly discovered, judged, and killed or ostracized in more stable, small-scale societies. This may also explain why the United States has a higher rate of psychopathy (c. 3.6%—Grant et al., 2004) than Europe (c. 0.7% in Oslo—Torgersen, Kringle, & Cramer, 2001)—the European psychopaths emigrated and found a good mating niche (cf. Cooke & Michie, 1999; Cooke, Michie, Hart, & Clark, 2005). This may also be why American academics, suffering their share of unpunished psychopaths in faculty meetings and university administration, tend to overestimate the likely reproductive success of prehistoric psychopaths.

Second, Driscoll also makes the interesting suggestion that individuals with Down or Williams syndromes might be considered more virtuous in some respects than “normal” people, despite their severe neurogenetic disorders. This is true for a few “Christian” virtues (sociability, friendliness, empathy) in Williams syndrome (Jones, Bullugi, Lai, Chiles, Reilly, Lincoln, & Adolphs, 2000; Mervis & Klein-Tasman, 2000). Also, individuals with Down syndrome show lower aggressiveness, antisocial behavior, property destruction, attention seeking, lying, and stealing compared to age- and IQ-matched individuals with other neurodevelopmental disorders but not compared to normal individuals (Chapman & Hesketh, 2000). However, Down and Williams syndromes rarely lead to conspicuous “pagan” virtues such as magnanimity, heroism, altruism, conscientiousness, patience, or norm-enforcement or to epistemological virtues such as intelligence, integrity, or wisdom. On the contrary, Down syndrome is associated with increased selfishness (“demandingness”), hyperactivity, anxiety, depression, and social withdrawal (Chapman & Hesketh, 2000; Roach, Orsmond, & Barratt, 1999). Williams syndrome tends to produce a loquacious over-gregariousness that, though more benign in the short term, taxes the patience of family and friends much as a narcissist or bore would. These are some reasons why individuals with these syndromes have trouble attracting mates.

Also, these syndromes are rare: about 1 in 500 for Down syndrome even in populations with age-delayed fertility profiles (Wald, Rodeck, Hackshaw, Walters, Chitty, & Mackinson, 2003), and 1 in 7,500 births for Williams syndrome (Stromme, Bjornstad, & Ramstad, 2002). Prehistoric hunter-gatherer tribes (with younger mothers and unsentimental attitudes toward infanticide of newborns with craniofacial abnormalities) might have encountered a sexually mature individual with one of these syndromes only once in every ten or twenty generations.

Costly signals need not be 100% reliable to evolve. If good brains and good genes show good statistical associations with moral virtues, then the latter can serve as a good indicator of the former. I have not demonstrated that all good brains show moral goodness or that all moral goodness issues forth from good brains. However, I did review substantial evidence that almost all mental health problems and intelligence-reducing neurodevelopmental disorders tend to undermine both the Christian and the pagan virtues.

Third, Driscoll's most important criticism of my costly signaling model is that the putative indicator trait (e.g., a moral virtue) must be the most efficient possible trait for an observer to assess, out of all possible traits that might advertise certain components of phenotypic or genetic quality. Such optimization reasoning is appropriate for most kinds of adaptations, but not for signaling adaptations, because signal evolution is highly stochastic and path dependent. This is why every animal species has a different set of fitness indicators and why taxonomists routinely use sexual ornaments (including genital morphology and courtship displays) to categorize animals. Sexual selection is a major source of biodiversity precisely because the demands of costly signaling vastly underspecify the precise design details of fitness indicators (Todd & Miller, 1997). Any indicator will do, as long as it is costly, complex, and hard to fake. This is a strength of costly signaling theory because it gives the theory very broad applicability, but it is a weakness because it makes almost impossible any a priori predictions about the design details of indicators in particular species. We can recognize an indicator post hoc when we see one, but we may have never been able to predict which indicators would evolve in which lineages.

Fourth, in a related point, Driscoll argues that the fitness information conveyed by moral virtues could be assessed more easily and reliably through other cues, such as verbal intelligence. True, if the set of phenotypic traits and genes advertised through moral virtues were precisely equivalent to the set of traits and genes advertised through verbal intelligence, then the virtues would be redundant signals. On the other hand, if there were no overlap between the traits and genes advertised by these two fitness indicators, one could not claim that they tap into a common construct of "fitness." The information they convey must overlap a bit, but not too much—like questions in a well-constructed personality scale or athletic events in a decathlon. This is a basic principle of psychometrics: more indicators yield more information. My challenge in this paper was

to show that moral virtues do indeed tap into general fitness traits such as intelligence, mental health, and brain efficiency; apparently I went too far in making the virtues sound redundant as fitness signals. Of course, the existence of many individuals with high intelligence but low moral standards (e.g., promiscuous novelists, narcissistic professors, corrupt politicians, some lawyers and journalists) suggests that cognitive abilities do not overlap entirely with moral virtues.

Fifth, Driscoll mentions that mate preferences for moral virtues may have arisen as a side effect of other prior selection pressures for morality (e.g., favoring mates whose offspring will thrive given strong reciprocity, in-group norms, and punishment mechanisms) or as a side effect of a general preference for safety and well-being in sexual relationships (e.g., favoring mates who are nice rather than nasty partners). These offer reasonable alternative launchpads for getting mate preferences for moral virtues off the ground.

The question remains: once there is a fitness benefit for favoring sexual partners who seem like good strong reciprocators and/or nice partners, would these mate preferences not impose sexual selection on such traits? This is a generic problem with apparently parsimonious explanations of mate preferences as side effects of other preferences—such hypotheses rarely take the next step and consider the resulting sexual selection pressures. If prehistoric hominids routinely favored sexual partners who seemed likely to be nice rather than nasty, then they would have imposed sexual selection for niceness—over and above any other selection pressures that favored niceness.

Sixth, Oliver Curry develops a fascinating account of the virtues as conflict-resolution devices. It is a complementary costly signaling account: whereas I focus on intersexual selection (mate choice), Curry focuses on intrasexual rivalry (conflict, dominance, and submission). Both processes were probably important in human evolution, so both imposed selection pressures for certain kinds of moral virtues as costly signals of superiority or of submissiveness. His account is especially good at accounting for (1) the disjunction between pagan virtues (superiority signals) and Christian virtues (submissiveness signals), (2) the submissive, dove-like qualities of many religious practices, and (3) the functional and behavioral similarities between many human virtues and animal conflict-resolution signals. Both of our theories seem pretty good at explaining supererogatory acts (conspicuously virtuous behavior that goes beyond the call of duty) by drawing attention to the social-signaling and reputational benefits of such acts for mate attraction and rival intimidation.

Seventh, Curry's dominance/submission focus sheds new light on some aspects of human courtship that I had not considered before. Courtship in many societies (and in many animal species) requires an extraordinarily complex, dynamic alternation between dominance signals and submission signals. A male must approach a female confidently and assertively yet show cues of deference, innocuousness, and respect for her power of mate choice. A female must test a male's fitness and resolve by resisting his current advances, yet inviting further attempts. This is not sexist stereotyping, but *Animal Behavior* 101. Pure dominance does not provoke sexual attraction, nor does pure submissiveness. Frequent subtle reversals of romantic power and dominance seem the most exciting. The skilled, socially intelligent, maximally virtuous lover can switch from hawk to dove and back again within one kiss. This is the basic plotline in many sexual fantasies (Leitenberg & Henning, 1995), in female-oriented romance novels (Salmon & Symons, 2004), in ritualized sex play involving bondage, domination, sadism, and masochism (Baumeister, 1997), and in copulation itself. These aspects of courtship seem to involve a sort of metadisplay of signaling prowess: male and female demonstrate their mastery of the conflict-resolution signals through continually testing each other's dominance and submissiveness. Those who are poor at such metadisplay may seem too pushy or wimpy, too ardent or cool; they may adopt alternative sexual strategies that get diagnosed as "courtship disorders" such as paraphilias (exhibitionism, frotteurism, voyeurism) or crimes (stalking, harassment, rape; Freund & Seto, 1998). Thus, mate choice may favor displays of one's ability to modulate dominance/submission signals quickly, creatively, and adaptively, as a reliable indicator of intrasexual conflict-resolution skill.

