

Krebs, D. L. & Janicki, M. (2002). Biological foundations of moral norms. In M. Schaller & C. Crandall (Eds.), *Psychological Foundations of Culture*.

Biological Foundations of Moral Norms

Dennis Krebs & Maria Janicki
Simon Fraser University

Abstract: All people acquire beliefs about how they should and should not behave. When such beliefs are adopted by most members of a culture, they constitute moral norms. How do moral norms originate and spread? Why do people preach them and behave in accordance with them? Why are some moral norms universal, and others relative to particular cultures? In this chapter we argue that to answer such questions, we must attend to the biological foundations of the mental mechanisms that give rise to moral norms and other aspects of culture.

COMMON CONCEPTIONS OF BIOLOGICAL AND CULTURAL FOUNDATIONS OF MORALITY

If you ask laypeople where they get their morals, they will give you such answers as, "Morals are taught to us at a young age by our parents directly and by society indirectly." "Morals are passed on to us via overt direction (e.g., be kind to others) and less overt means, such as imitation." "People learn morals from social custom and conformity to group norms." If you ask laypeople what role-inherited dispositions play in the acquisition of morality, they will probably answer, "little or none." Indeed, most laypeople believe that to become moral people must be taught to resist the temptations of the flesh, to oppose their animal instincts, and to suppress or sublimate their natural urges.

Laypeople who harbor such Original Sin conceptions of human nature are in good company. Consider the conclusions reached by the following eminent evolutionary theorists:

The behavioral dispositions that produce complex social interdependence and self-sacrificial altruism must...be products of culturally evolved indoctrination that has had to counter self-serving genetic tendencies.... The commandments, the proverbs, the religious "law" [i.e., moral norms] represent social evolutionary products directed at inculcating tendencies that are in direct opposition to the "temptations" representing, for the most part, the dispositional tendencies produced by biological evolution (Campbell, 1978, pp. 52-53).

Be warned that if you wish, as I do, to build a society in which individuals cooperate generously and unselfishly toward a

common good, you can expect little help from biological nature. Let us try to teach generosity and altruism, because we are born selfish (Dawkins, 1989, p. 3).

An Evaluation of Cultural-indoctrination-Social-learning Models of Moralization

It would be foolish to deny that cultural indoctrination and social learning play important roles in the acquisition of morality. We teach children to behave in accordance with the moral norms of their cultures, and children copy the moral behaviors of adults. However, in their traditional forms, cultural indoctrination and social learning models of moralization fail to explain (a) where the moral norms of cultures came from in the first place, or how they originated, (b) how people decide what norms to preach and what behaviors to sanction, (c) why people conform to some moral norms and deviate from others, and (d) why some norms are universal, whereas others are unique to particular cultures.

Implicit in Original Sin-Cultural Indoctrination models of moralization is the idea that biology and culture, or nature and nurture, constitute separate and independent sources of behavior, each opposing the other. We should know by now that such nature-nurture dichotomies are misguided. Cultural indoctrination and social learning are mediated by mechanisms in our brains, and our brains are evolved structures that are shaped by environmental experiences. To understand how the mechanisms that produced moral norms operate, we need to understand the adaptive functions such mechanisms performed in ancestral environments.

THE EVOLUTION OF MORALITY

Because moral norms pertain largely to the ways in which people should and should not treat one another, we would expect the adaptive problems that the mechanisms that give rise to moral norms were designed to solve to be social in nature. The biological reason why species acquire the adaptations necessary for sociality is because aggregating and living in groups fosters their fitness (that is to say, chances of surviving, reproducing, and propagating their genes) better than living alone. Benefits of sociality may include enhanced defense against predators (including hostile members of one's own species), enhanced ability to acquire food and other resources (for example through group hunting and trading), and enhanced ability to mate. Significant among the potential costs of sociality are increased competition for resources. Humans are among the most social of all animals. A spate of evidence suggests that adaptations that enabled our hominid ancestors to foster their fitness in cooperative ways played a pivotal role in the evolution of the human species (e.g., Leakey & Lewin, 1977; Tooby & Devore, 1987).

Reaping the benefits of sociality and cooperation gives rise to an inevitable dilemma, which the philosopher John Rawls (1971) describes well in the opening pages of his book, *Theory of Justice*:

Although a society is a cooperative venture for mutual advantage, it is typically marked by a conflict as well as by an identity of interests. There is an identity of interests since social cooperation makes possible a better life for all than any would have if each were to live solely by his own efforts. There is a conflict of interests since persons are not indifferent as to how the greater benefits of their collaboration are distributed, for in order to pursue their ends, each prefers a larger to a lesser share.

Evolutionary theory leads us to expect members of groups to be evolved to try to induce other members of their groups to behave in ways that helped their hominid ancestors propagate their genes. One way of achieving this goal is for members of groups to reward others when others behave in ways that benefit them biologically, and to punish others when others behave in ways that reduce their chances of surviving and reproducing. Another way is for members of groups to persuade others to behave in ways that advance their (the persuaders') interests.

The Adaptive Functions of Administering Sanctions and Making Moral Judgments

When theorists who advance cultural indoctrination models of morality assert that culture or teaching is the source of morality, they are defining culture primarily in terms of the moral judgments members of cultures preach and the moral sanctions they administer. Socializing agents teach children to conform to the moral norms of their culture by giving them moral instruction, by rewarding them when they are good, and by punishing them when they are bad. Adults induce members of their societies to conform to moral norms by indoctrinating them and by administering sanctions such as ostracism, fines, and incarceration. The difference between cultural indoctrination models and evolutionary models is that the latter do not cast those who preach morality and administer sanctions as motivated to moralize recipients for the sake of morality. Evolutionary models view the moral judgments people preach to each other as outputs from evolved mechanisms designed to induce recipients to behave in ways that advanced the biological interests of senders in ancestral environments.

When people preach moral judgments to others, they are engaging in a form of communication. Biological analyses of communication in nonhuman species have revealed that most of the signals animals send to each other are manipulative, and many are deceptive (Dawkins, 1989; Mitchell & Thompson, 1986). Humans' large brains and resultant ability to plan, simulate events mentally, and take others' perspectives (referred to as "mind-reading" by some psychologists), expand immensely their capacity to manipulate and to deceive others, as does their capacity for language. From a biological perspective, the function of moral judgments (and other aspects of culture) is to induce recipients to behave in ways that foster the interests of senders (cf. Cronk, 1995 and Flinn, 1997).

There are two types of moral judgment, which philosophers have labeled aretaic and deontic. Aretaic moral judgments characterize people or acts as good or bad. We imagine that the precursor to the first moral judgment made in the human species was some paralingual signal communicating disapproval of a selfish or harmful act, or approval of an altruistic or cooperative act. Darwin (1871) believed that "love of praise and dread of blame" played key roles in the evolution of morality in the human species. From a biological perspective, aretaic moral judgments constitute social sanctions designed to control the behavior of those who are being judged.

Deontic moral judgments prescribe that people should or should not behave in particular ways. People usually buttress deontic moral judgments with reasons: “you should behave morally because....” Many of the reasons people invoke to support moral norms involve explicit or implicit promises of reward or threats of punishment. Viewed biologically, such reasons constitute arguments designed to persuade recipients to behave in accordance with the prescriptions they are invoked to support.

The Adaptive Functions of Conforming to Moral Norms and Copying the Normative Behaviors of Others

It is easy to understand why self-interested senders would preach moral norms and administer sanctions to those who uphold and violate them, but why would self-interested recipients conform to moral norms? Evolutionary theory leads us to expect an answer such as, because the mechanisms that mediate such conformity enhanced their fitness. The fitness-enhancing benefits of a mechanism containing a decision-rule such as, “repeat behaviors that were followed by rewards (delivered by others) and stifle behaviors that were followed by punishment”—that is to say, a mechanism designed in terms of the principle of reinforcement—are obvious. A potentially more adaptive decision-rule is, “anticipate the consequences of your acts and emit those with the greatest potential to advance your interests.” Two important sources of information about potential consequences are (a) promises of reward and threats of punishment, and (b) perception of the consequences of acts performed by others. Social learning mechanisms such as vicarious learning, modeling, and conformity enable individuals to avoid the costs of trial and error learning. As stated by Bandura (1986), “Because people can learn approximately what to do through modeling before they perform any behavior, they are spared the costs and pain of faulty effort. The capacity to learn by observation enables people to expand their knowledge and skills on the basis of information exhibited and authored by others” (p. 47). (See Boyd and Richerson (1995) for mathematical models comparing the fitness enhancing effects of individual learning and social learning.)

Evolutionary theorists have characterized social learning mechanisms as “a kind of special purpose adaptation constructed to selectively acquire information and behavior by observing other humans and inferring the mental states that give rise to their behavior” (Henrich & Boyd, 1998, p. 217). The question is, how is this adaptation designed? Some

theorists believe that evolved mechanisms that mediate modeling and conformity are relatively indiscriminating. For example Simon (1990) has argued that a trait he calls “docility,” defined as the disposition to learn what others teach you and to believe what others want you to believe, evolved in the human species through the enormous fitness benefits it conferred on those who inherited it. Simon (1990) notes that the complexity of the world and the boundedness of human rationality prohibit people from independently evaluating every fact or suggestion they encounter. He suggests that people can be induced to behave altruistically because the costs of conforming to altruism-inducing words and deeds are outweighed by the “advantageous knowledge and skills acquired through docility” (p. 1667). Thus, according to Simon, (1990) social learning-cultural indoctrination mechanisms are designed in ways that induce people quite indiscriminately to conform to the words, and copy the deeds, of others.

Other evolutionary theorists believe social learning mechanisms are designed in significantly more discriminating ways than described by Simon (1990). For example, the biologists Flinn and Alexander (1982) have suggested that evolved social learning mechanisms are guided by the following decision-rules: “imitate those who appear successful” and “behave oppositely to those who don’t”; “accept advice and instruction from those with an interest in one’s success” and “view skeptically advice and instruction from those with conflicting interests with regard to the topic being instructed”. Boyd and Richerson (1985) have suggested that social learning mechanisms are affected by three “biases”, which they have labeled indirect biases, direct biases, and frequency-dependent biases. Indirect biases are similar to the decision-rules described by Flinn and Alexander. They induce people to copy the words and deeds of people who seem fit, are admired, respected, of high status, wise, and so on. Direct biases induce people to evaluate (consciously or unconsciously) the alternative beliefs or behaviors that are available, and select those that they believe will best foster their fitness. The criteria used to evaluate alternative beliefs or behaviors may be genetically inherited, learned from one’s own experience, or learned from others (Boyd & Richerson, 1985). Frequency-dependent biases induce people to copy the words and deeds that are most frequent in the population.

Empirical evidence supports the idea that social learning mechanisms are biased in the sorts of ways hypothesized by evolutionary theorists. Studies have found that the probability of modeling is affected by

factors such as the similarity between the model and observer, the status of the model, the nurturance of the model, the extent to which the model controls resources, vicarious learning, and rewards and punishments (Burton & Kuncze, 1995, pp. 151-152). Evolutionary theory supplies a framework for interpreting such piece-meal, empirically-derived findings.

Implications for the Evolution of Moral Norms

The idea that moral norms evolve through an interaction between the moral judgments, examples, and sanctions transmitted by senders who are evolved to advance their biological interests and the reactions of recipients who are evolved to advance their biological interests has several implications. First, people should attempt to invoke the moral norms with the greatest potential to benefit them, and there is evidence they do. Many investigators have found that people interpret moral norms in ways that foster their interests (Bandura, 1991; Batson, 1999; Krebs & Laird, 1998). As examples, Damon (1977) found that children faced with the task of distributing a resource such as an extra piece of pizza tended to invoke norms that favored their interests, and Leventhal and Anderson (1970) found that adults who contributed the most to tasks tended to invoke norms of equity that justified dividing resources in their favor.

Second, if people transmit moral norms to influence others, they should tailor the norms in ways that enhance their persuasive impact. As an examples, we would expect senders to tailor moral norms to the cognitive sophistication and values of recipients, and the evidence suggests they do (for example, see Carpendale & Krebs, 1992). Although we would expect senders be evolved to exhort recipients to perform more altruistic and self-sacrificial acts than recipients are inclined to perform, as Original Sin-Cultural Indoctrination models of morality imply, we would not expect exhortations such as, “you should always sacrifice your interests for me” to have much persuasive impact. Inasmuch as the reactions of recipients determine whether transmitted judgments pay off for those who send them, recipients become agents of selection, in effect selecting the moral judgments that evolve. The inevitable result of the interaction between the vested interests of senders and the vested interests of receivers are moral norms that implicitly or explicitly preach, “we should foster our interests in ways that foster the interests of others, or at least do not harm them”, and “we should behave in ways that foster our mutual interests.” Do unto others as you would have them do unto you.

Third, we would not expect recipients to conform passively to the moral norms preached by others when the norms in question do not advance their interests. When people’s interests differ, we would expect arguments and negotiations to occur, with each partner modifying his or her position in an attempt to find mutually-beneficial common ground. This is exactly what we found in our research on moral conflicts experienced by couples in their everyday lives (Krebs, Denton, Wark, Couch, Racine, & Krebs, in press). Note that philosophers such as Habermas (1984) believe that the best way to make truly moral decisions is through such negotiation and debate.

Finally, if moral norms are tools designed to solve the adaptive problems that arise when self-interested individuals seek to maximize their gains in social exchanges, we would expect the moral norms that people preach and practice to vary in accordance with the type of relationship they have with recipients and the accompanying confluences and conflicts of interest. We are not surprised by evidence that children adopt different norms in relations with adults than they do in relations with peers, as many developmental psychologists have found (see Krebs & Van Hesteren, 1994, for a review). We also are not surprised that social psychologists have found that adults tend to invoke more individualistically self-serving norms in relations with strangers than in relations with friends (Greenberg, 1978), that friends tend to invoke norms of equality (Austin, 1980), and that marital partners tend to invoke norms upholding mutual gratification of needs (Greenberg & Cohen, 1982). Clark, Mills, and Powell (1986) have distinguished between “exchange relationships” in which people invoke equity norms that enable them to balance their costs and benefits, and more intimate “communal relationships”, in which people invoke more altruistic and needs-based norms. Social psychologists have attributed differences in the norms people invoke to variations in the “outcome interdependencies” (i.e., conflicts and confluences of interest) of the types of relationship in question. Like social psychological analyses, our analysis of the evolution of moral norms implies significantly more situational variation in the moral norms people invoke than expected in psychological theories such as those espoused by cognitive-developmental theorists, and the evidence supports this expectation (see Krebs, Denton, Vermeulen, Carpendale, & Bush, 1991; Krebs, Denton, & Wark, 1997; and Krebs, Vermeulen, Carpendale, & Denton, 1991, for reviews).

Note that on our analysis there are no clear boundaries between biological and cultural determinants of moral norms. Biology (evolved mechanisms) shapes culture (moral norms). Culture originates in the evolved minds (biology) of people. Evolved mechanisms induce those who invent culture to transmit it to others. Evolved mechanisms in recipients determine whether they copy it and transmit it to others. Once generated, culture may shape evolved mechanisms. As examples moral norms that constrain reproduction, prescribe ostracism, and uphold capital punishment may become agents of natural selection. Boyd and Richerson (1992) have demonstrated that virtually any norm can evolve if members of groups punish those who fail to conform to it as well as those who fail to punish the nonconformists.

HOW FIVE UNIVERSAL MORAL NORMS EVOLVED

If, as we have argued, humans are naturally-inclined to conform to moral norms that enhanced the fitness of their hominid ancestors, it follows that, contrary to Original Sin models of human nature, we believe humans may be naturally-inclined to behave in moral ways, and thus be good by nature. Indeed, we believe such natural inclinations shaped several universal moral norms. It follows that we do not believe there is any necessary inconsistency between behaving morally and pursuing one's biological interests. That people are naturally-inclined to foster their prospects of surviving, reproducing, and propagating their genes does not necessarily imply that they are born bad. Morality pertains to the *ways* in which people pursue these goals. On our analysis, it is moral to pursue one's biological interests in ways that are beneficial to others—that is to say, in mutually-beneficial ways—, and immoral to pursue one's biological interests in ways that are destructive to others.

We turn now to a more detailed discussion of the evolution of behavioral dispositions that underlie five universal moral norms--norms that prescribe obedience to authority, reciprocity, care, social responsibility, and solidarity (Boehm, 2000; Brown, 1991; Colby and Kohlberg, 1987; Darwin, 1871; Gouldner, 1960; Sober & Wilson, 1998; Snarey, 1985; Wright, 1994). Each norm pertains to a different type of social relationship and is invoked for different reasons. Norms upholding obedience pertain to hierarchical relationships, and are invoked to avoid punishment. Norms of reciprocity pertain to egalitarian exchange relations among peers, and are

invoked to foster gains in trade. Norms prescribing care and altruism pertain to communal, affectionate bonds among friends and relatives, and are invoked to foster long-term fitness-enhancing relationships. Norms of social responsibility and solidarity pertain to relations between individuals and their groups, and are invoked to uphold fitness-enhancing systems of cooperation. We will explain how upholding each of these norms could have helped our ancestors propagate their genes in mutually-beneficial ways.

For the sake of this discussion, assume the following: (a) behaviors that conform to or are consistent with moral norms are the products of evolved decision-making rules, or genetically-based behavioral strategies, (b) a variety of such strategies existed in ancestral populations, (c) these strategies competed against one another and against immoral strategies, and (d) each strategy produced replicas of itself in proportion to its competitive success. The genes that fostered winning strategies increased in frequency, and the genes that fostered losing strategies decreased in frequency until they went extinct. We will explain how the strategies implicit in the five moral norms we will consider could have won such evolutionary contests. In particular, we will explain how they could have defeated the selfish strategies that Original Sin theorists believe reigned supreme.

It is important to note that it is the relative success of different strategies in particular populations that guides evolution. Although variants that win such evolutionary contests may be considered the best of those against which they have competed, they need not be the most optimal or the best imaginable. As we will explain, moral behavioral strategies that would maximize benefits to every member of a group if adopted by all members of a group may nonetheless be defeated by more selfish strategies that enhance the relative fitness of particular members. Ironically, as selfish strategies increase in frequency, they may lower the absolute fitness of all members of a group. Note also that the adaptive consequences of specific acts—that is to say, their effects on biological fitness—are less important than the cumulative or net consequences of the strategy, disposition, or mechanism that gives rise to the acts over the life-time of the actor. No strategy is successful all the time.

When people think of genetically-based behavioral strategies, they tend to assume a higher degree of genetic determinism than we want to imply. Genes provide instructions for building proteins that create physical structures that house mental mechanisms. Genes do not control behavior directly; they are not

puppet masters, pulling our strings. They influence behavior indirectly, by “programming” mental mechanisms with decision-rules or strategies that on balance gave rise to behaviors that enhanced the biological fitness of those who inherited them. Such behaviors are not controlled by the genes themselves; they are mediated by an interaction between stimuli from the environment and the mental mechanisms built by genes.

It is important to acknowledge the important role the environment plays in the creation, design, and operation of evolved mechanisms. First, the environment supplies the raw materials for building mental structures. Second, inputs from the environment may supply triggers that turn mechanism-creating or mechanism-transforming genes on and off at various points during the life cycle of animals. Third, environmental stimuli may shape evolved mechanisms to respond to particular types of information and to ignore others. Fourth, environmental experiences early in life may calibrate or program the decision-making rules in psychological mechanisms, which may induce individuals who inherit the same genes but grown up in different environments to invoke different behavioral strategies. Finally, environmental stimuli activate evolved mechanisms and supply information that guides the decisions they produce. For these and other reasons, Crawford and Anderson (1989) have characterized evolutionary psychology as an “environmentalist discipline.”

Obedience Norms

Universal moral norms prescribing obedience to authority are reflected in exhortations to honor one’s parents, supplicate oneself before gods, listen to one’s elders, and obey the orders of one’s leaders. We believe that dispositions to obey authority stem from evolved predispositions to defer to more powerful members of one’s group.

In the conflicts of interest that inevitably occur between members of groups, the adaptiveness of the strategy one adopts will be contingent on one’s relative power. Relatively powerless members of groups face a Hobson’s choice: either defer to those who are more dominant than they are, or get beaten up or killed by them. We would expect deferential strategies to evolve when they contributed more to an individual’s biological fitness than more aggressive or blindly selfish strategies. When the prospects of future benefits for subordinates are sufficiently promising, deferring to more dominant members in the present will often be their most adaptive strategy.

Deference enables subordinates to avoid the costs of fighting a losing battle, enabling them to make the best of a bad situation and to live to fight another day.

The social relations of many species are organized in dominance hierarchies or pecking orders. Members of groups determine in low-cost ways who is more powerful than whom, and accommodate to the resulting status. In such species, the costs of deference to more dominant members of groups may be compensated by the gains of dominating those who are lower in the pecking order. Deferential strategies have evolved in many nonhuman species (Alcock, 1998). With respect to moral norms, we would expect dominant members of groups to preach obedience norms to weaker members, and we would expect weaker members to accommodate behaviorally, believing it is right, and in their interest, to do so. See Boehm (2000), Krebs (1998, 2000b), and Sloman and Gilbert (2000) for more extended discussions of the adaptive value of deference.

Ontogenetic implications. In Piaget’s (1932) pioneering research on moral development, he found that young children view morality primarily in terms of obedience to authority. Piaget labeled the moral orientation of young children, “the morality of constraint”. The cognitive-developmental psychologist, Kohlberg (1984) also found that young children define morality in terms of “avoidance of punishment and the superior power of authorities” (p. 18). From our perspective, the reason why young children espouse and conform to norms prescribing obedience to authority is because young children are among the weakest and most vulnerable members of groups. Deference to adults is their most adaptive strategy.

Cognitive-developmental psychologists such as Piaget and Kohlberg also have found that as children grow older and interact more frequently with peers, they change their moral orientation from the morality of constraint to a more egalitarian “morality of cooperation” and “instrumental exchange” in which they uphold norms of reciprocity.

Norms of Reciprocity

The adaptive potential in upholding norms of reciprocity is easy to see. As explained by Piaget (1932), reciprocity enables peers to resolve conflicts of interest in mutually beneficial ways, such as taking turns. Members of all social species inevitably need help from each other and want things others possess. Through gains in trade, individuals who adopt

cooperative strategies that induce them to reciprocate resources and assistance may well do better than individuals who treat each other selfishly. This does not, however, guarantee the evolution of reciprocity. Although two reciprocating individuals may acquire more resources than two selfish individuals, a selfish individual interacting with a reciprocator may come out ahead by taking without giving in return. To evolve, cooperative strategies must contain antidotes to exploitation by selfish strategies.

One cooperative strategy that contains a built-in antidote to selfish exploitation is called tit for tat. It is based on the decision-rule, "make a cooperative overture, then copy the response of your partner in subsequent interactions". In computer simulations of natural selection, Axelrod and Hamilton (1981) found that the tit for tat strategy could defeat more selfish strategies—that is to say, replicate at a faster rate—if it "invaded" populations in clusters (thus enabling the strategy to reap the benefits of interacting with itself). Tit for tat is a powerful strategy because it opens the door to a string of mutually beneficial exchanges with cooperative partners in its first move, but quickly cuts its losses against selfish partners on subsequent moves. Trivers (1971, 1985) and Dugatkin (1997) have reviewed evidence that tit for tat strategies have evolved in nonhuman animals. There is a spate of evidence that norms of reciprocity have evolved in all human cultures (Gouldner, 1960; Wright, 1994).

Ontogenetic implications. Piaget (1932) attributed the change in children's moral orientation from obedience to cooperation to changes in their social relations—from relations with adults to peer relations. Kohlberg (1984) has asserted that when children begin believing in norms of reciprocity, they stop believing in norms of obedience. From a biological perspective, we are not surprised that research has failed to support this assertion (see Krebs & Van Hesteren, 1994, for a review of relevant research). We would expect people to retain the beliefs and behavioral strategies they acquire early in life when such beliefs and strategies are biologically useful later in life. For this reason, we are not surprised to find adults preaching obedience to authority when they are in positions of power, and conforming to exhortations to obey authority when they are in subordinate positions, as they did in Milgram's (1964) classic experiments (Newitt & Krebs, in preparation). We also are not surprised that adults such as the Hatfields and McCoys and social groups such as the Protestants and Catholics in Ireland get into childish and self-defeating tit for tat type blood feuds. We would expect people to be

naturally disposed to invoke and to conform to the moral norms with the greatest promise of fostering their fitness in the contexts in question. Thus, we would expect far more situational variation in moral norms espoused and practiced than cognitive-developmental theorists assume (see Krebs, Denton, Vermeulen, Carpendale, & Bush, 1991; Krebs, Denton, & Wark, 1997; and Krebs, Vermeulen, Carpendale, & Denton, 1991, for elaborations of this expectation evidence supporting it).

Care-based and Altruistic Moral Norms

Caring for friends. As children grow older, they begin to form enduring friendships. Tooby and Cosmides (1996) have pointed out that exchanges between friends are not usually based in the sorts of tit for tat decision-rules invoked by young children and adults toward strangers. Friends do not expect to be paid back for each and every perk they bestow on each other. Cognitive-developmental theorists have found that, unlike young children who view morality in terms of reciprocal exchanges, teenagers and adults believe that people should help their friends and relatives when they are in need. We believe norms prescribing care and altruism toward friends and relatives are universal. In explaining how behavioral strategies upholding such norms could evolve, Tooby and Cosmides (1996) allude to a phenomenon called the bankers' paradox: Banks are least likely to lend you money when you need it the most. To resolve adaptive versions of the bankers' paradox, individuals invest in friends whom they expect to be there for them when they are in need. In this sense, upholding friendships is like buying an insurance policy. In a similar vein, Nesse (1999) and Frank (1988) have suggested that close relationships are based in emotional commitments rather than in tit-for-tat type strategies. Although commitments to friends may seem counter to selfish interests in the short-term, Nesse (1999) argues that they pay off better than more selfish strategies in the end.

Caring for mates. People from all cultures also believe that mates are morally obliged to care for each other. Evolutionary theory has no difficulty explaining the selection of normative strategies that induce individuals to care for their mates. Inasmuch as members of the opposite sex are able to select their mates, they would be expected to select mates who are naturally inclined to care for them and their kin. Thus, strategies that induce individuals to care for their mates could evolve through sexual selection (see Krebs, 1998, for an elaboration of this process).

Caring for kin. In the final tally, mating counts little in evolution if the offspring from sexual unions fail to survive and to reproduce. No one is surprised by evidence from the animal kingdom of parents sacrificing their individual interests for the sake of their offspring, because such self-sacrificial behaviors help parents propagate their genes. In a classic paper, Hamilton (1964) pointed out that the biological value of parental investment can be extended to relatives other than offspring. The probability of individuals sharing genes varies in proportion to their degree of relatedness: 50% for parents and offspring; 50% for full siblings; 25% for cousins, and so on. Hamilton (1964) explained how a decision-rule could evolve that induces individuals to help others when the coefficient of their relationship is greater than the cost to the helper of helping, divided by the benefits to the recipient ($r > c/b$). Given the genetic benefits of helping relatives, we would expect individuals to be biologically predisposed to discriminately help kin over non-kin, and for such dispositions to be reflected the moral norms of all cultures.

Norms of Social Responsibility

Tit for tat forms of reciprocity pertain to direct, dyadic exchanges. It is easy to see that benefits to members of groups could be increased through the gains in trade made possible by more indirect forms of reciprocity. For example, if all members of a group helped those they were most qualified to help, or if they gave resources they needed the least to those who needed them the most, every single member of the group could come out ahead. To achieve such benefits, members of groups could take on tasks they were especially skilled at accomplishing, giving rise to divisions of labor in which people took on the roles they were best equipped to perform.

There are, however, two obstacles to the evolution of strategies that dispose individuals to fulfill their social responsibilities in ways that enable everyone in their group to maximize their gains through indirect reciprocity. First, it is more difficult to catch those who fail to fulfill their responsibilities than it is to catch those who cheat on more direct exchanges. Second, members of groups have less incentive to punish those who fail to fulfill their social responsibilities than they do to punish those who exploit them directly. To evolve, socially responsible strategies must contain mechanisms designed to catch and to punish cheaters (Axelrod, 1984; Boyd & Richerson, 1992). The evolutionary biologist Alexander (1987) hypothesized that systems of

indirect reciprocity could evolve if members of groups (a) shared information about the selfish and altruistic behaviors of others through gossip and other means, (b) favored those who behaved altruistically, and (c) discriminated against those who behaved selfishly. In recent game theory research, Nowak and Sigmund (1998) supported Alexander's hypotheses. Nowak and Sigmund (1998) created a computer simulation of evolution in which behaving altruistically (that is to say, in socially-responsible, cooperative ways) enhanced an individual's reputation or "image," and behaving selfishly degraded it. These investigators found that if socially responsible members of groups favored those with a good reputation, socially-responsible strategies could evolve, become evolutionarily stable, and support systems of indirect reciprocity.

The problem of appearance. We believe Nowak and Sigmund's (1998) model is limited in at least one important respect. When these game theorists set the parameters for their evolutionary contests, they programmed the images that observers formed of members of their groups to be valid. However, if being viewed as socially responsible and altruistic pays off, it would be in people's interest to fool others into believing they are more socially responsible and altruistic than they actually were. Instead of actually fulfilling their social obligations or actually sacrificing their needs for others, they could act like they were behaving in socially responsible and altruistic ways. If such impression-management strategies enabled people to reap the rewards of indirect reciprocity without paying the price, they could destroy the system of cooperation upon which they preyed. To evolve, all strategies must contain antidotes to strategies designed to exploit them.

A spate of evidence supports the idea that we humans inherit mechanisms designed to manage the impressions we make on those in positions to affect our welfare (Jones, 1990; Leary, 1995). We are all actors at heart, as Goffman (1958) so eloquently described in his classic, *Presentation of Self in Everyday Life*. Fortunately, however, there are constraints on the evolution of impression-management strategies. First, it is difficult, or impossible, to act in socially responsible ways without behaving in socially responsible ways, in public, at least. Second, false impressions constitute adaptive problems for the recipients they are designed to manipulate. Inasmuch as being fooled is maladaptive, mechanisms designed to resist being fooled should evolve. Thus, we would expect a sort of arms race in which actors acquire mechanisms that induce them to present themselves as more moral

than they really are, observers acquire mechanisms to detect such deceptions, and so on. See Alexander (1987), Cosmides & Tooby (1992), Krebs (1998, 2000a, c), Trivers (1985) for an elaboration of this process.

Norms of Solidarity and Patriotism

All cultures contain moral norms that exhort individuals to sacrifice their immediate interests for the sake of their groups. One way in which dispositions that gave rise to such norms could have evolved is through the biological benefits of indirect reciprocity, as we have explained. In addition, such dispositions may have evolved through a controversial process called group selection. In *Decent of Man*, Darwin (1871) considered this possibility, writing:

A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase. (p. 500)

The idea underlying group selection is that the benefits that altruistic individuals bestow on others who possess replicas of their “altruistic genes” may enable such strategies to evolve. In effect, the altruistic strategies help themselves by helping others who possess replicas of them. Note that the process of group selection is similar to the process of kin selection because both processes are based in the biological benefits individuals accrue when they help others who share the genes (that is to say, the strategies) disposing them to help. Because the strategy of helping all members of one's group is less discriminatory and less nepotistic than the strategy of helping one's kin, it more moral, but less likely to evolve.

The evolutionary obstacle to strategies that dispose individuals indiscriminately to help members of their group is, of course, that selfish members of the group (i.e., those who reap the benefits bestowed by the altruists without suffering the costs of behaving

altruistically) fare better than the altruistic members. As put by Darwin (1871):

It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those who were the most faithful to their comrades, would be reared in greater numbers than the children of selfish and treacherous parents belonging to the same tribe....[i.e., within the group]. Therefore it hardly seems probable that the number of men gifted with such virtues...could be increased through natural selection....

Sober and Wilson (1998) have suggested that group-upholding strategies (thus norms) could evolve through group selection, but they acknowledge that such strategies could evolve only in special conditions, such as when the frequency of altruists varies across groups, altruistic groups fare better than selfish groups, and the altruistic and selfish groups eventually mix in the population. Could this have happened in the evolutionary history of our species through, perhaps, tribal wars? There is a spate of psychological evidence that humans quickly and deeply identify with groups to which they are even arbitrarily assigned, and favor the members of their in-groups over the members of out-groups (see Hornstein, 1978; Krebs & Denton, 1997; Tajfel, 1982, and Tajfel & Turner, 1985 for reviews of supporting research). Whether such dispositions and strategies evolved through group selection or through some other mechanism, such as the benefits of indirect reciprocity, remains to be determined.

Reconceptualizing Kohlberg's Theory of Moral Development

Readers familiar with Kohlberg's (1984) theory of moral development may have noticed a parallel between the universal moral norms we been discussing and the types of behavior prescribed at each of Kohlberg's stages of moral development. This is no coincidence. We believe the moral judgments that define Kohlberg's stages of moral development uphold the evolved strategies we have been considering. In contrast to Kohlberg, however, we believe the reason why people of different ages tend to uphold different strategies is because they tend to face different kinds of adaptive problem.

Implications and Qualifications

We have argued that the decision-rules implicit in the behaviors upholding the five moral norms we have

considered could well have constituted winning strategies in ancestral environments. As such, they could have evolved to become normative in the human species. We believe such norms have, in fact evolved, and that they are culturally universal. If humans are naturally-inclined to behave in moral ways, cultural norms prescribing moral behaviors would support, rather than oppose, evolved dispositions. From a biological perspective, beliefs such as it is right to obey authority and people are morally obligated to help their friends are functionally similar to beliefs such as it is right to foster your safety and security. People harbor moral beliefs because believing in the strategies or forms of conduct prescribed by such beliefs paid off better than believing in other strategies or forms of conduct. Viewed in this way, the pragmatic connotations of words such as "should" and "ought" make sense. When people say things like, "you should be loyal to your friends", they imply both that it is morally correct and that it will pay off in the end.

It is important to recognize that we are not saying that people are genetically programmed to emit the strategies implicit in moral norms as fixed action patterns. Moral strategies are based in decision-rules that are contingent on executive mechanisms and a complex array of environmental cues. In effect, people decide which, of the many strategies available to them will work best in the situations they encounter. As examples, we would expect decisions about deferring to and obeying authority to be contingent on estimates of the power of the authorities, the value of the resources in question, and the probability of reaping rewards and avoiding punishments. Decisions about upholding one's end of reciprocal exchanges should be guided by such factors as the relative costs of giving and receiving and the probability of future exchanges (Axelrod, 1984). Relationship-upholding strategies should be sensitive to factors such as the extent to which people anticipate needing help in the future, the number of alternative relationships available to them, the anticipated costs and benefits of cheating, and so on (Tooby & Cosmides, 1992).

UNIVERSAL AND CULTURALLY-RELATIVE MORAL NORMS

We have been focusing on universal moral norms that we believe have evolved in all cultures. Tooby and Cosmides (1992) have labeled universal aspects of culture metaculture. They have suggested that metaculture evolved through an interaction between the evolved mechanisms possessed by our hominid ancestors and the regularities in the social and

physical environments of human societies that existed during the Pleistocene. We know, however, that cultures may differ significantly in the particular moral norms they adopt.

Tooby and Cosmides (1992) attribute some cross-cultural variations in norms to what they call "evoked culture". Different norms evolve in different cultures because different environmental inputs impinge on the same evolved mental mechanisms of their members. Consider food-sharing for example. Anthropologists have found that moral norms upholding cooperative food-sharing tend to evolve in hunter-gatherer societies in which the probability of success on a hunt is variable, but not in societies in which the probability of each individual obtaining food by gathering is more consistent (see Cosmides & Tooby, 1992). As another example, differences in cultural norms about which foods are edible may result from differences in the ecological conditions affecting food quality, variability, and availability. Henrich and Boyd (1998) have suggested that mechanisms of conformist transmission (a frequency-dependent bias discussed above) may play an important role in maintaining cultural differences between groups.

THE EVOLUTION OF NON-ADAPTIVE AND MALADAPTIVE MORAL NORMS

To this point, our analysis of the biological foundations of moral norms has been highly adaptationist. We have traveled a considerable distance on the back of the assumption that the psychological mechanisms that give rise to moral norms evolved because they fostered the fitness of our ancestors. It is now time to acknowledge that it is also possible for non-adaptive and maladaptive norms to evolve.

Let us first consider the radical position advanced by Dawkins (1989). Dawkins (1989) suggested that genes have built machines (i.e., brains) that have freed themselves from their creators, much like computers, once programmed, may acquire the ability to think for themselves. In contrast to the units of biological evolution—genes—, Dawkins has termed the units of cultural evolution "memes". Examples of memes are ideas, songs, stories, inventions, fashions, and norms. Dawkins has suggested that memes compete against each other for space in people's minds. Some are selected, transmitted to other minds, increase in frequency and evolve; others are rejected and go extinct. In contrast to biological evolution, which progresses at a glacial slow pace, cultural evolution may occur with great

rapidity, as manifest in the growth of slang terms and changes in fashion. Dawkins believes that cultural evolution has become uncoupled from biological evolution; thus, it is a waste of time to search for the fitness-enhancing sources or effects of cultural memes.

Although Dawkins' point may be valid with respect to fads and fashions such as hoola hoops, baseball caps worn backwards, and culturally-specific moral norms that bear little relation to the fitness of those who adopt them, we do not believe it pertains to the types of universal moral norm we have been considering. To quote Buss (1999):

Because "information" emanating from other individuals in one's social group is limitless, a potentially infinite array of ideas compete for the limited attention span of humans. Evolved psychological mechanisms in the receivers must sift through this barrage of ideas, selecting only a small subset for psychological reconstruction. The subset that is selectively adopted and internally reconstructed in individuals depends on a foundation of evolved psychological mechanisms. (p. 406)

This is not, however, to deny that non-adaptive and maladaptive moral norms may evolve as byproducts of the social learning mechanisms we have considered. For example, all three biases described by Boyd and Richerson (1985) could give rise to maladaptive norms. With respect to direct biases, people may misjudge the consequences of the choices available to them. Specific choices, such as whether or not to model the moral norms of a religious group, may have long-term negative consequences that are impossible to anticipate (Richerson & Boyd, 1989). With respect to indirect biases, people may copy behaviors of high status models that evoke negative reactions from others. For example teenagers living in conservative communities may suffer from copying the moral norms displayed or advocated by rap stars. Models also may manipulate observers into adopting norms that advance the interests of the models. With respect to frequency-dependent biases, although evolved behaviors and beliefs are, by definition, common, maladaptive behaviors and beliefs such as those pertaining to drug-taking could grow in popularity even though they ultimately decreased the fitness of those who modeled them.

And even if, as we have argued, the evolved social learning mechanisms and behavioral dispositions we have considered gave rise to adaptive moral norms in the environments in which they were selected, there

is no guarantee that such mechanisms and dispositions will give rise to adaptive behaviors in current environments. As examples, mechanisms that disposed our hominid ancestors to imitate group members who were admired for their hunting skills, fighting ability, possession of resources, and popularity may, in modern environments, induce individuals to imitate the maladaptive behaviors of celebrities such as Mike Tyson. Mechanisms that disposed our ancestors to obey powerful authorities may be manipulated in modern environments by charismatic cult leaders. Mechanisms that disposed our ancestors to reciprocate, invest in friends, be faithful to their mates, and support their relatives may give rise to maladaptive behaviors in modern environments, where people are able to move to new locations, change groups frequently, and develop relationships over the Internet (see Janicki & Krebs, 1998, for a more extended discussion of evolutionary approaches to culture).

SUMMARY AND CONCLUSION

To understand culture, one must understand the mechanisms that generate and refine it. In this chapter, we argued that the mental mechanisms that give rise to moral norms and other aspects of culture evolved because they helped our hominid ancestors reap the benefits of sociality. Children acquire moral norms through social learning and cultural indoctrination, but to understand such processes, we must understand the ways in which they were shaped by natural selection. The reason why people preach moral norms, administer sanctions, conform to moral norms, and copy normative behaviors is because such practices were biologically beneficial in ancestral environments. Our analysis of the evolution of moral norms implies (a) that people will attempt to induce others to invoke the moral norms that benefit them the most, (b) that people will tailor the moral norms they preach to others in ways that enhance their persuasive impact, (c) that recipients will be disposed to conform to the moral norms that best advance their biological interests, and (d) that people in different kinds of relationship will preach and practice different moral norms. Although we disagree with Dawkins' (1989) conclusion that it is a waste of time to search for the fitness-enhancing sources or effects of moral norms and other cultural memes, we acknowledge that non-adaptive and maladaptive moral norms may evolve as byproducts of social learning mechanisms.

Moral norms differ cross-culturally because people from different cultures face different kinds of adaptive problem. Universal moral norms

prescribing obedience to authority, reciprocity, care, altruism, social responsibility, solidarity and patriotism evolved in all cultures because they helped our ancestors solve universal social problems. The reason why the moral norms people invoke vary across age, type of relationship, and social situation is because adaptive problems vary across age, relationships, and situations. Decisions about whether or not to behave in morally normative ways are contingent on a complex array of environmental cues.

We need to purge nature versus nurture conceptions of the relation between biology and culture from the social sciences forever. Culture originates in, is transmitted by, and is propagated through mental mechanisms that evolved through natural selection. Evolved mechanisms shape culture, which in turn may shape the evolved mechanisms that produce it. In contrast to the widely-held idea that the function of moral norms is to constrain our animal instincts, we believe that moral norms stem from and reflect natural dispositions to behave in moral ways.

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