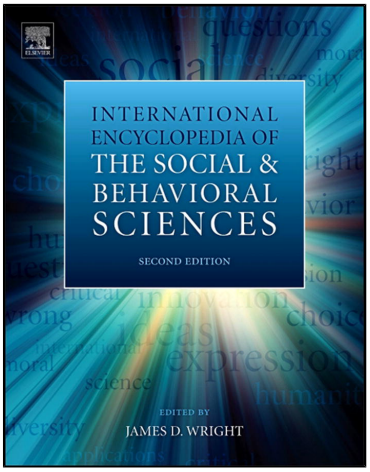

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Morality: Evolution of

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Abstract

This article looks at the origins of human morality, and examines the contributions of both biological evolution and cultural evolution. Biological evolution may help explain certain categories of moral behavior (such as altruism), as well as certain morally relevant capacities (such as empathy). Cultural evolution may explain how different moral systems emerge in different times and places, and why they tend to foster aspects of human nature that enhance group success and discourage aspects of human nature that undermine it. Morality must be understood as the joint production of both biological and cultural evolution.

> The ant, the bird, the marmot… have read neither Kant nor the fathers of the Church nor even Moses. The idea of good and evil has thus nothing to do with religion or a mystic conscience. It is a natural need of animal races. And when founders of religions, philosophers, and moralists tell us of divine or metaphysical entities, they are only recasting what each ant, each sparrow practices in its little society.
>
> —Peter Kropotkin (1898), *Anarchist Morality*.

Morality Is a Mess

This might seem like a strange place to begin a discussion of the origins of morality, but let me explain why I think it's a useful starting point. Scientists strive for simple, parsimonious explanations for phenomena. Those that meet this standard are described approvingly as *elegant* explanations. It seems unlikely, however, that morality will ever have an elegant explanation, for the simple reason that morality is not an elegant phenomenon. Like many human institutions, it is a messy aggregation of a vast array of competing influences. These influences include inclinations rooted in the biology of human nature, such as a tendency to favor kin, a tendency to resent freeloaders, and a capacity to empathize with the suffering of others. They also include influences that can be classified broadly as cultural. Among these are norms designed to rein in socially disruptive aspects of human nature, norms aimed at furthering the interests of the individuals or groups promoting them, and – at least occasionally – genuine efforts to work out the logical consequences of universal principles of justice and the common good. If we focus on any of these influences to the exclusion of the others, we will arrive at a lopsided view of the nature of morality – hence the importance of keeping in mind that morality is a mess.

In this article, I consider both the biological and cultural evolution of our formal moral systems. I begin with the evolution of altruistic behavior, which is the area of moral behavior that evolutionary theory has shed the most light on. I then consider some of the putative evolved mechanisms underlying human morality, such as inhibitions against harming innocents, the capacity for empathy, and an aversion to incestuous mating. Finally, I consider the cultural evolution of morality and why some moral systems thrive and persist whereas others fade away.

The Problem of Altruism

In 2011, the Australian state of Queensland suffered extreme flooding. As with any disaster, this one left many tales of heroism in its wake. Among the most poignant is the story of 13-year-old Jordan Rice. Jordan had been shopping with his mother and his younger brother, Blake. As they drove home, they were caught in a flash flood. They ended up on the roof of their car, stranded precariously in the middle of raging waters. Eventually, help arrived. A local man tied a rope to himself and made his way to the car to try to rescue the family. Jordan insisted that the rescuer save his little brother first. Before the rescuer could return, Jordan and his mother were swept away and drowned.

By putting his brother ahead of himself, Jordan lost his life. This act of selflessness represents the height of moral action. But from a simplistic Darwinian perspective, it is puzzling. At first glance, evolutionary theory seems to imply that the organisms that survive and leave behind the most descendents will be those that look after number one. That's exactly what Jordan Rice didn't do. How could natural selection have spared a tendency for such self-sacrificial behavior? Of course, we might wonder whether natural selection is relevant to the question; perhaps Jordan was simply brought up in a culture that prizes self-sacrifice. But that is probably not the whole story, because comparable acts can be found in other animals. For instance, birds in some species feign injury to lure predators away from their babies in the nest, only attempting a getaway at the very last minute. Likewise, bees sting invaders to the nest, protecting the colony but losing their lives in the process. Self-sacrificial altruism is surprisingly common in nature. What might be going on?

Kin Selection

Over the past half-century, evolutionary biologists have made great strides in answering this question (Alexander, 1987; de Waal, 2006; Krebs, 2011). The single-most important theory of animal altruism – and the one most relevant to the examples given above – is William Hamilton's (1964) *kin selection theory* (*see* Kin Selection; Kinship, Evolution of). According to standard neo-Darwinian theory, a gene can be selected if it has effects that boost its replication rate relative to rival versions of the same gene (Dawkins, 1976). This can happen in a number of circumstances. Most obviously, it can happen if the gene increases its bearer's chances of surviving and reproducing. But it can also happen if the gene increases *another* organism's chances of surviving and reproducing, as

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long as the other organism is more likely than chance to possess the same gene. Close relatives are more likely than chance to possess any given gene, and thus a tendency to help close relatives can potentially be selected. This process is called *kin selection*. Kin selection is the explanation for feigned injury in birds: The heroic bird's babies in the nest are more likely than chance to carry any genes contributing to the development of injury feigning. Kin selection is also the explanation for the suicidal nest defense of bees and other eusocial insects: Their close kin in the nest are more likely than chance to carry any genes contributing to the nest defense tendency. And kin selection may be an important part of the explanation for Jordan's sacrifice: His brother was more likely than chance to possess genes contributing to whatever motivations and inclinations underpinned his selfless behavior. Of course, shared genes were the last thing on Jordan's mind; he was merely acting on his inclinations. But kin selection is plausibly part of the explanation for how those inclinations evolved in the first place. Needless to say, the relationship between kin selection and morality is far from simple. After all, moral systems tend to oppose certain forms of kin altruism: those we label 'nepotism.' Nonetheless, kin selection helps to explain a class of behavior that we typically view as moral: altruism among kin.

Reciprocal Altruism

Hamilton's theory explains most of the altruistic behavior seen in other animals. However, it does not explain most of the altruistic behavior seen in human beings, because much of this involves nonrelatives. Certainly, the kind of extreme altruism exemplified by Jordan Rice may be more common among kin than nonkin. But more common, less costly forms of altruism in our species often take place between unrelated people (Stewart-Williams, 2007). Nonkin altruism is hard for the evolutionist to explain, but there are various possibilities. The best known is Robert Trivers' (1971) *reciprocal altruism theory* (*see* Sociobiology: Overview). This starts from the fact that individuals working together can often produce more than the sum total of what each could produce working alone. If five hunters working together bring down one giraffe, for example, they end up with more meat per hunter than if each working alone brings down one turtle. Thus, cooperation is better for all involved. Reciprocal altruism utilizes this principle but smears the cooperation out across time: I help you when I can; you help me when you can. This sounds like a good arrangement, so why don't all animals do it? The main stumbling block is *the problem of cheating*. Although it is better to trade favors than to act selfishly, it is better still to reap the benefits of someone else's help but then not return the favor. Because cheating pays more than mutual helping, mutual helping is evolutionarily unstable. It is displaced easily by a tendency to exploit helpers. The only way that mutual helping could evolve is if it coevolves with psychological 'machinery' that somehow defends against cheats. According to Trivers, many of our standard-issue emotional responses do exactly this. People unconsciously keep track of favors given and received, and when a trading partner (e.g., a friend or ally) starts taking advantage, people naturally respond with anger and moral indignation. This motivates them to punish the cheat or to cut off further aid, which protects them from exploitation. These and other psychological dispositions can be viewed as an evolved moral psychology (see also Cosmides and Tooby, 1992).

Trivers' theory has been tested in various ways. Most notably, it has been explored *in silico* – that is, using computer simulations (Axelrod, 1984; Axelrod and Hamilton, 1981; Nowak and Sigmund, 1992). In a typical simulation, virtual organisms encounter one another repeatedly and must either cooperate or defect (i.e., cheat). Points are awarded based on how well they do in each encounter. The virtual organisms are programed with various strategies, from very simple ones (such as Always Cooperate or Always Defect) to very complex, conditional ones. Among the most successful strategies, and by far the most famous, is Tit-for-Tat. Tit-for-Tat works like this. The first time it encounters a new player, it cooperates. In every subsequent encounter, it simply does whatever the other player did the last time they met. If the other player cooperated, Tit-for-Tat cooperates, thereby continuing a mutually beneficial cooperative partnership. If the other player defected, Tit-for-Tat defects, thereby cutting off the option of further exploitation. Tit-for-Tat is not always the most successful strategy; it all depends on who it's up against. But the general picture emerging from this research is that strategies *like* Tit-for-Tat – strategies that cooperate conditionally but defend against cheats – tend to do better than overly nice or overly nasty strategies.

Reciprocal altruism appears to be relatively rare among nonhuman animals, although there is evidence for it in vervet monkeys (Seyfarth and Cheney, 1984) and vampire bats (Wilkinson, 1984), among others. In contrast, many lines of evidence suggest that reciprocal altruism is an important part of the explanation for nonkin altruism among humans (see, e.g., Delton et al., 2011; Gurven et al., 2000; Hames, 1987).

Sexual Selection

Reciprocal altruism is not the only contender, however. A more recent attempt to explain our altruistic streak is based on an older theory: sexual selection theory (Darwin, 1871). Sexual selection is a form of natural selection. It occurs when a trait is selected, not because it enhances its bearer's survival prospects, but because it increases its bearer's *reproductive* prospects – that is, its ability to attract mates or outcompete same-sex rivals for mates. According to sexual selection theory, the mate choices of one sex can give rise to elaborate sexual ornamentation in the other. The enormous nose of the male proboscis monkey is a striking example. Females prefer to mate with males with larger-than-average noses. This preference, acting over many generations, gives rise to the male's impressive proboscis. In humans, not only the females but the males as well possess 'ornaments' that the other sex finds attractive (Stewart-Williams and Thomas, 2013). This includes secondary sexual characteristics such as women's hour-glass shape and breasts, and men's V-shaped torso and deep voice (Barber, 1995). According to some evolutionary psychologists, sexual selection has also produced behavioral ornaments, and among these are altruism and morality (Miller, 2007; Zahavi, 1975). These traits are costly, hard-to-fake displays of fitness, designed by selection to attract mates (*see* Human Mate Choice, Evolution of). Geoffrey Miller has made

the strongest case for altruism and morality as sexually selected ornamentation. The following quote is from his book *The Mating Mind*:

> Murder, unkindness, rape, rudeness, failure to help the injured, fraud, racism, war crime, driving on the wrong side of the road, failing to leave a tip in a restaurant, and cheating at sports. What do they have in common? A moral philosopher might say they are all examples of immoral behavior. But they are also things we would not normally brag about on a first date. (Miller, 2000: p. 292)

Several lines of evidence support the sexual selection theory of altruism. First, just as female proboscis monkeys prefer males with enormous noses, men and women tend to prefer mates who display kindness and generosity (Buss, 1989). Second, men are particularly likely to provide help in circumstances where doing so might demonstrate their fitness and enhance their mating prospects. So, for example, men are more likely than women to help when helping is dangerous and an audience is present, especially when the recipient of the help is a woman (Eagly and Crowley, 1986; Johnson, 1996). In a similar vein, Hawkes (1991) has made a strong case that big-game hunting is at least partly a matter of men showing off to obtain mates. The spoils of the hunt are not channeled preferentially to kin or used to pay off earlier debts; instead, the meat is shared widely throughout the group. What explains this altruistic sharing? According to Hawkes, the best hunters tend to have higher status and more wives and more affairs than other men – a finding that fits well with the sexual selection hypothesis. Certainly, sexual selection could not be the whole explanation for human altruism. It does not apply to altruism among kin, for instance, as kin are not potential mates (except in rare and unfortunate cases). But there is enough evidence now to think that sexual selection may be one piece of the puzzle.

Group Selection

The final theory of altruism we'll consider is also the most controversial. This is the idea that altruism is not a product of selection among individuals, but rather of selection among groups. The concept of group selection traces back to Darwin (1871) who, in *The Descent of Man*, suggested that groups of altruists would fare better than groups of selfish individuals, and thus that altruism would slowly displace selfishness. The subject was brought to center stage nearly a century later, when V.C. Wynne-Edwards (1962) argued that organisms in many species had evolved to sacrifice themselves for the good of the group. The main impact of Wynne-Edwards' work was to inspire a strong counterargument. Critics like G.C. Williams (1966) pointed out that any organisms that sacrificed themselves for the group would quickly be displaced by those that sat back and let others make the sacrifice while they pumped out as many offspring as possible. Although the critics conceded that group selection was possible in principle, most concluded that it was unlikely in practice. During the 1960s and 1970s, the idea that adaptations evolve for the good of the group was largely expunged from evolutionary biology, and replaced with the idea that adaptations evolve for the good of individuals and their kin (Dawkins, 1976; Williams, 1966).

After several decades in the wilderness, however, a more sophisticated form of group selection is now gaining attention (Nowak, 2006; Sober and Wilson, 1998; Wilson, 2012). Modern group selectionists do not claim that group selection is the only selective force, and thus the approach is probably better named *multilevel selection theory*. Advocates of this theory (e.g., Wilson and Sober, 1994) distinguish between within-group selection and between-group selection. Within-group selection favors traits that advantage the individual, but between-group selection favors traits that advantage the group. Organisms, it is claimed, are the net outcome of these countervailing forces. When there are small differences in reproductive success within groups, but big differences in average reproductive success between groups, selection is concentrated at the level of the group. According to the multilevel selectionists, this is precisely what has happened in our species. As such, we have an evolved tendency to extend help not only to relatives but to nonrelatives in our group, even when they cannot reciprocate, and even when there is no scope for sexual or reputational benefits (a phenomenon known as *strong reciprocity*; Gintis, 2000).

Although group selection is currently enjoying a new lease of life, so too are criticisms of the theory. Some critics charge that group selectionists are too willing to attribute any instance of human sociality and cooperation to group selection (Pinker, 2012). Humans are certainly prosocial animals, but prosociality is not necessarily selected for the good of the group. As the theories described above show, it can be selected instead for the good of prosocial individuals and their kin. And there are several reasons to favor individual-level selection over group-level selection as the explanation. First, the individual-level approach has been much more empirically fertile than group selection. Second, in many ways, humans do not look like we're strongly group selected (Pinker, 2012; Price, 2012). Parents spend many thousands of dollars each year on their children, but if they also give several hundred dollars to charity, this is considered uncommonly altruistic (Singer, 1981). Grandparents routinely look after their grandchildren without payment; nonrelated group members generally do not. People happily share with family and friends, but they have to be cajoled and coerced to pay their taxes. If humans were strongly group selected, why would we need tax collectors? Why would we need conscription? Why would we need ethical codes that admonish us to prioritize the interests of the group? Certainly, extreme altruism among nonrelatives is hard to explain in terms of individual-level benefits – consider, for instance, the soldier who throws himself on a grenade to save the rest of the group. But such acts are rare, and it is usually a mistake to invoke natural selection to explain rare acts. Of course, group selectionists have responses to all of these criticisms, and the issue remains as yet unresolved. But with persuasive arguments on both sides, the group selection debate is currently one of the most exciting debates within evolutionary behavioral science (*see* Human Cooperation, Evolution of).

A Mind Made for Morality

Until recently, altruism was the main area in which Darwinian theory has been used to explore moral psychology. But altruism

is only one component of morality, and over the past decade or so, evolution-minded thinkers have begun exploring others. In the process, they have started to shed light on some of the psychological mechanisms underpinning moral behavior. So, for instance, according to Jonathon Haidt's *Moral Foundations Theory* (Haidt and Joseph, 2004), the human mind comes factory equipped with a set of moral tastes, including a desire to reduce the suffering of others, a sense of fairness, loyalty to the in-group, emotions and attitudes guiding behavior toward people of lower versus higher status, and a desire for purity and the avoidance of contamination. Other thinkers have focused on moral emotions, such as guilt, shame, contempt, anger, disgust, compassion, and sympathy (de Waal, 1996; DeScioli and Kurzban, 2009; Rozin et al., 1999). In this section, I discuss four putative psychological mechanisms underpinning human morality – namely, inhibitions about harming other people, the capacity for empathy, a sense of fairness, and an aversion to incest.

Trolleyology

Arguably, the most famous contemporary research in moral psychology is based on a hypothetical moral dilemma imported from philosophical ethics. The dilemma – which has been described as the white lab rat or the fruit fly of moral psychology – involves an out-of-control trolley (i.e., train) careening down the track and heading toward five workers on the line. You are standing there watching, and you realize that if the trolley continues on its present path, it will kill the five workers. In one version of the dilemma, you just so happen to be standing next to a lever. If you pull the lever, it will divert the trolley to another line, saving the five. Unfortunately, there is one person on the other line, and that person will be killed instead. What do you do? If you're like most people, you divert the trolley, killing one person but saving five (Hauser et al., 2007). But now imagine a second scenario. You are standing on a footbridge over a railway track, watching the trolley hurtle toward the five workers. This time you cannot divert it. Standing next to you, however, is a fat man (or, if you prefer, a man with a heavy backpack). Somehow you calculate that, if you push the man onto the track, his weight will be sufficient to stop the trolley in its tracks before it kills the five – but the man will die in the process. You are not heavy enough to stop the trolley, so you cannot make the ultimate Wynn-Edwardsian sacrifice and throw yourself on the track instead. What would you do in this situation? If you're like most people, you would *not* push the man (Hauser et al., 2007). But from a utilitarian perspective (according to which the right action is the one that produces the greatest good for all involved), the two dilemmas are morally identical: Either one person dies or five die. Why do we respond so differently?

Joshua Greene and colleagues (2004) have argued that people have a built-in aversion to directly and intentionally harming innocent people, and that, as a result, they are willing to pull the lever but not push the man. It is a matter of debate whether such an aversion is a product of natural selection as opposed to learning or culture. But the fact that the pattern is so widespread across cultures has led many to the former view. Interestingly, although people's decisions do not differ a great deal across cultures, their *explanations* for them do (Hauser et al., 2007). This suggests that, to some extent, moral training simply furnishes us with rationalizations for an unreasoned aversion that we would possess anyway (see Haidt, 2001).

Empathy

Closely related to this is the capacity for empathy. Empathy involves understanding what others are experiencing and having the appropriate emotional responses to it – for example, sympathizing with others' suffering (Baron-Cohen, 2011). Although culture and experience may amplify or diminish our empathetic tendencies, there are several reasons to suppose that the basic capacity for empathy is a product of natural selection. For one thing, the first flowerings of empathy appear very early in the life span (Warneken and Tomasello, 2009). As Paul Bloom has observed, toddlers often become upset if a nearby adult is upset, and they may even offer up a teddy bear or favorite blanket to make the adult feel better. In addition, some nonhuman animals may be capable of empathy. The strongest case has been made for large, intelligent animals like chimpanzees and dogs (de Waal, 1996). However, some researchers have argued that even mammals as diminutive as rats have some rudimentary capacity for empathy (Bartal et al., 2011). Patricia Churchland (2011) suggests that empathy originally evolved to allow mammalian mothers to attend to the needs of their offspring. In some lineages, however, natural selection later co-opted the neural mechanisms underpinning maternal empathy and applied them to other social relationships, including relationships with mates, unrelated allies, and ingroup members.

Although empathy is an important ingredient for morality, by itself it is not sufficient for morality. Indeed, as various commentators have pointed out, empathy can sometimes be morally misleading (e.g., Bloom, 2013). We easily empathize with our friends and neighbors' smallest hurts but may fail to empathize with the millions of people starving in the developing world. Thus, doing the right thing sometimes involves going against the advice of our empathy and listening instead to the voice of reason. But although empathy is not sufficient for morality, it is hard to imagine that someone who lacked empathy entirely could be truly moral (Prinz, 2005). Empathy is an important building block of human morality, and one that plausibly has its origin in our evolutionary history.

A Fairness Instinct?

A more contentious claim is that human beings have a built-in sense of fairness – a 'fairness instinct,' as David Barash put it. The most common way of exploring this issue is a decision task known as the Ultimatum Game. The game involves two players: the Proposer and the Responder. The Proposer is given a sum of money – say, $10. Her task is to propose how that money should be split between herself and the Responder. The Proposer could suggest a 50–50 split, or a 90–10 split, or any other combination. Then it's the Responder's turn. The Responder has only two options: accept the proposal or reject it. If he accepts it, they both get the proposed sums of money. If he rejects it, no one gets anything. In a world where people were perfectly rational and entirely self-interested, Proposers would

elect to keep $9 and give away only $1, and Responders would accept any nonzero offer – why opt for nothing when you could have $1? But that is not what usually happens. In Western nations, Proposers usually offer $4–5, and Responders usually reject anything less than $3. The Proposers are not acting irrationally; they know that if they make a lowball offer, the Responder will resent it and reject it, so they make an offer the Responder will accept. The Responders, in contrast, *are* acting irrationally, because their insistence on punishing unfair offers leaves them out of pocket. That, at any rate, is the verdict of classical economics. But closer inspection suggests how this tendency could be adaptive. For most of our evolutionary history, humans rarely encountered people they would never encounter again. A willingness to respond angrily to unfairness – in this case, to reject a stingy offer even at some personal cost – signals to the world that you are not the sort of person who will accept mistreatment. Although this may be self-destructive in the short term, it may be beneficial in the longer term, as it means that people will think twice about mistreating you next time around.

Thus, the Ultimatum Game findings have been used as evidence for an evolved distaste for unfairness. The problem is, though, that the results described so far come exclusively from Western nations. When Joseph Henrich and colleagues (2005) took the Ultimatum Game to 15 small-scale societies, they found that people in these societies behaved very differently than Westerners. Among the Machiguenga horticulturalists of Peru, for instance, Proposers often made low offers – and Responders often accepted them. Even more surprising, among the Au and Gnau of Papua New Guinea, Proposers often made *high* offers – offers of up to 70% of the pot – and Responders turned them down! Henrich concluded that the alleged fairness instinct is actually a set of cultural norms: norms that grow up in cultures that are embedded in a market economy and in which people must cooperate closely to eke out a living.

The issue is further complicated by the fact that other researchers have found evidence for an incipient sense of fairness in nonhuman animals. Brosnan and de Waal (2003) trained capuchin monkeys to exchange pebbles for food. Sometimes the capuchins received pieces of cucumbers for their pebbles; sometimes they received grapes. The monkeys preferred the grapes, but they were quite happy to receive the cucumber – as long as their neighbor was only getting cucumber, too. However, if the neighbor started getting grapes, while they continued to get cucumber, the capuchins threw a tantrum. Indeed, they often threw the cucumber away forcefully. The monkeys were not perturbed by inequality per se. Some collected more stones than others and therefore earned more treats, but onlookers did not throw tantrums about that. Instead, they were upset that another individual got a better reward for the same behavior. In other words, they didn't want an equal distribution of wealth; they wanted equal pay for equal work. The capuchin sense of fairness is a far cry from our own. For one thing, capuchins only object to unfairness when they are on the receiving end of it (although see Brosnan et al., 2010). Nonetheless, the fact that these less culture-bound creatures possess anything like a sense of fairness makes it harder to believe that our own sense of fairness is purely a cultural invention. Although it is not yet clear how to reconcile the capuchin findings with the cross-cultural Ultimatum Game findings, the solution may relate to the fact that the term 'fairness' is being used in subtly different ways in the different studies. In the Ultimatum Game, it means equality (i.e., a 50–50 split); in the capuchin research, it means equity (i.e., equal pay for equal work). It may be that, rather than having an evolved aversion to deviations from a 50–50 split, humans have an evolved aversion to unfairness or mistreatment more generally, with some flexibility in what exactly this means from culture to culture (*see* Human Cooperation, Evolution of).

Incest Aversion

There may also be biological contributions to some aspects of our sexual morality. The best example concerns incest. In many species, our own included, inbreeding is highly detrimental to fitness. The offspring of incestuous liaisons often do not survive, and when they do, they have an elevated risk of genetic abnormalities. It is plausible to suppose, then, that we possess psychological adaptations that tend to steer us away from incestuous mating. Given the strong evolutionary rationale for such adaptations, it is probably no coincidence that most people feel acute disgust at the idea of sex with siblings or other family members. A powerful case has been made that humans have an evolved tendency to develop a sexual aversion to individuals they grow up with, especially during the first five or so years of life (Fessler and Navarrete, 2004; Lieberman et al., 2007). This negative sexual imprinting is known as the *Westermarck effect* (Westermarck, 1921; Wolf, 1995). Now it might be argued that incest aversion is a cultural invention: Perhaps earlier peoples observed that incestuous mating led to birth defects and the like, and therefore proscribed it. But this does not fit the facts. Societies have proscribed many forms of sexuality over the ages: adultery, premarital sex, and so on. Sometimes the proscription works; sometimes it does not. But when it does, it is usually because people manage to resist temptation, not because they're disgusted by the act in question. In contrast, most people are profoundly disgusted by the idea of incestuous mating, and they feel this way despite receiving little socialization against incest: Parents generally worry about their teenagers having sex with nonrelatives, not with siblings. It is plausible to suppose, then, that an aversion to incest is a product of natural selection. The moral precept 'Incest is wrong' is presumably *not* a direct product of natural selection. However, it may be an idea that we readily accept, given the nature of human nature (*see* Incest Prohibition, Origin and Evolution of).

The Cultural Evolution of Morality

This brings us to the topic of the cultural evolution of morality. Although some suggest that morality is a product of biological evolution – an adaptation like eyes and wings – there are several reasons to view it instead as the joint product of both biological and cultural evolution (Mesoudi and Danielson, 2008; Stewart-Williams, 2010). First, moral codes vary tremendously across cultures and times (Prinz, 2005). In modern Western societies, most people deem cannibalism, slavery, and torture to be self-evidently wrong; in earlier times, however, and across a wide range of cultures, they were

deemed morally permissible. Similarly, during the twentieth century, the West underwent a profound shift in modal attitudes to such issues as homosexuality, premarital sex, and the treatment of ethnic minorities. Certainly, there are still differences of opinion within Western culture: People disagree bitterly about the morality of abortion, capital punishment, casual sex, drug use, and euthanasia. But this too is difficult to square with the notion that morality is a direct product of biological evolution (although see DeScioli and Kurzban, 2009). A second reason to look beyond biology is the fact that morality often goes against the grain of our raw biological impulses. For instance, the principle that we should 'turn the other cheek' goes against the natural impulse to harm those who harm us. If turning the other cheek were biologically adaptive for our ancestors, we would presumably possess an evolved appetite for it. This is not to deny that, at least in some cases, morality simply reflects our natural inclinations; think, for instance, of our nepotistic streak and our aversion to incest. But often morality looks more like a set of cultural norms designed to put the brakes on socially divisive inclinations. A final reason to doubt that morality is a biological adaptation in any simple sense is the fact that we strive to teach our children to be moral. Although young children spontaneously help others in a way that even adult chimpanzees do not, parents and teachers still spend a lot of time encouraging children to share and not to hurt their playmates. They might not create children's prosocial tendencies out of nothing, but they clearly try to amplify them. Once again, this suggests that the norms and ideals we bunch together under the heading 'morality' must be understood as the joint production of both biology and culture.

In this final section, I examine three theories about how moral systems might evolve culturally: (1) the memetic approach, according to which moral ideas come to predominate in a group to the extent that they are good at replicating themselves; (2) cultural group selection, according to which moral ideas come to predominate in a group to the extent that they promote the group's interests; and (3) gene-culture coevolution, according to which cultural changes in moral ideas (or indeed any aspect of culture) can alter biological selection pressures and lead to downstream genetic change.

Moral Memes

The first approach to cultural evolution is the memetics approach. Richard Dawkins (1976) coined the term 'meme' to refer to a unit of culture: an idea, a word, a ritual, a tune. He then argued that, just as natural selection among genes favors genes that are good at replicating themselves, so too natural selection among memes favors memes that are good at replicating themselves. A central insight of the theory is that the memes that come to predominate in a culture are not necessarily those that are good for us. They *may* sometimes be good for us, but that's not the reason they are selected. Memes are selected because they are good for the memes themselves, where goodness is defined in terms of their ability to spread from mind to mind and to persist in a culture. Applied to morality, the claim would be that moral memes are selected not because they enhance reproductive fitness, or because they benefit individuals or groups, but instead because they are good at selfishly replicating themselves. The memetic approach does not necessarily conflict with the earlier material. Indeed, the earlier material may shed light on why some moral memes succeed whereas others fall out of the meme pool. Memes must adapt to relatively fixed aspects of human nature. So, for instance, a moral system that prohibited any form of nepotism – including the tendency to feed and clothe one's own offspring rather than the next-door neighbor's offspring – would be unlikely to persist in the meme pool, as it would clash too violently with our evolved kinship psychology. Moral memes must also adapt to the current cultural setting. The fairness meme, for instance, seems to prosper better in market economies than in small-scale societies.

The memetic perspective may help explain some otherwise-puzzling features of morality. Consider, for instance, the first four of the Hebrew 10 Commandments: have no Gods before me; make no graven images; do not take God's name in vain; and keep the Sabbath holy. These have nothing to do with harm avoidance, or justice, or any other major moral principle. At a push, it could be argued that they foster social cohesion. But the memes'-eye view raises an alternative and often-overlooked possibility: These commandments help to protect the religious system that they are a part of. They may be viewed as part of a large cluster of memes – a memeplex – 'designed' by memetic selection to perpetuate itself. Critics of memetics note that, thus far, the approach has yielded little in the way of empirical findings. Nonetheless, it is an appealing approach, which alerts us to the possibility that at least some moral memes may exist not because they help us, but simply because they help themselves.

Cultural Group Selection

A second approach to cultural evolution goes by the name of *cultural group selection*. This is selection for the good of the group, but at the level of cultural elements rather than genes. Richerson and Boyd (2004) argue that group selection at the genetic level was probably weak in our ancestral past, as there was too much gene flow between groups. There was much less 'meme flow,' however. Even today, neighboring forager tribes are often genetically indistinguishable, but speak mutually unintelligible languages. If this kind of asymmetry was typical throughout our evolutionary history, there would have been much greater scope for cultural group selection than for genetic group selection. The sociologist Emile Durkheim long ago suggested that institutions such as morality function as social glue, binding together large-scale societies. Cultural group selection provides a possible mechanism for bringing about such institutions.

Many aspects of morality are potentially explicable in terms of cultural group selection. One example is the Western institution of monogamy. The most common mating pattern in ancestral societies was a mixture of monogamous and polygynous marriage (Marlowe, 2003). As Henrich and colleagues (2012) note, though, several centuries ago, European cultures established a norm of monogamous marriage. This norm applies even to high-status men who, in traditional societies, would often have taken several wives. The monogamy norm cannot be explained as a direct product of natural selection; after all, it is historically recent and, to some extent, pushes

against our evolved tendencies. How, then, did it come about? Henrich et al. suggest that groups that instituted monogamous norms had a number of advantages over those that did not. For a start, crime rates and rates of violence are generally lower in monogamous than polygynous societies. This is because polygynous societies are overrun with bachelors – if one man has four wives, three men must have none – and when young men have no wives or mating opportunities, they are more likely to cause problems (Daly and Wilson, 2001). In contrast, groups adhering to the monogamy norm have fewer such problems. These groups were therefore more productive and wealthier. They grew faster and persisted for longer. Furthermore, other groups, observing their success, may have copied them. In this way, the monogamy meme spread – despite the fact that it clashed to some degree with human nature (*see* Marriage Systems, Evolution of).

Cultural group selection is probably not a complete explanation for morality. As the philosopher David Hume (1777/1999) pointed out, certain virtues – those he called the "monkish" virtues: celibacy, fasting, penance, and the like – are not useful for society in any obvious way. But cultural group selection does help to explain a deep trend in our moral systems: the fact that they generally encourage aspects of human nature that facilitate social harmony, and discourage aspects of human nature that upset it.

Gene-Culture Coevolution

The final approach – gene-culture coevolutionary theory – is distinguished by its emphasis on the interactions between biological evolution and cultural evolution (Cavalli-Sforza and Feldman, 1981; Durham, 1991; Lumsden and Wilson, 1981) (*see* Gene-Culture Coevolution). The classic example of gene-culture coevolution concerns the capacity to digest lactose in milk even after the age of weaning. This is found almost exclusively in populations with a long history of dairying. One might suppose that the capacity to digest lactose came first and that the cultural practice (dairying) followed. It seems, however, that it was the other way around: Dairying came first and established a selection pressure that led to the evolution of life-long lactose digestion (Laland et al., 2010). A similar process may have shaped human morality. Richerson and Boyd (2004) suggest that gene-culture coevolution helps explain why humans are so much more altruistic and prosocial than other animals (see also Boehm, 2012). In their view, our hypertrophied altruism stems originally from cultural group selection (*see* Human Cooperation, Evolution of). Groups that established and enforced altruistic norms did better than other groups, lasting longer and growing more rapidly. Once the prosocial norms were in place, though, people whose genes fitted them to this social milieu prospered and had more offspring. In time, the relevant genes crowded out competing variants. Thus, biological evolution reinforced the cultural tendency and amplified our altruistic dispositions.

Conclusion

Morality is a complex phenomenon that resists any simple explanation. It is the net outcome of a tangle of conflicting causal influences. These include both biological and cultural influences. Biology affects morality in various ways. First, some forms of moral behavior, in particular altruism, have their origin in our evolutionary history. Second, formal moral systems sometimes reflect aspects of human nature. This includes, for example, the proscription on incest among biological relatives. Third, certain evolved capacities provide the basic building blocks for morality. This includes the capacity for empathy and emotions like anger, disgust, and guilt. And fourth, biology may constrain our moral systems: Moral systems that conflict too violently with human nature may be unlikely to persist.

In addition to these biological influences, cultural evolution may help to explain the moral systems that crop up in different places and times. Ultimately, moral memes must possess properties that enable them to stick around in the culture. In many cases, the property in question may be the fact that they enable groups holding those moral memes to prosper and persist. Finally, not only does biology shape morality but morality may shape biology. It may do this by setting up selection pressures that, over many generations, fit people to the demands of the local moral system.

See also: Cultural Evolution: Overview; Cultural Evolution: Theory and Models; Gene–Culture Coevolution; Human Cooperation, Evolution of; Incest Prohibition, Origin and Evolution of; Incest, Inbreeding, and Their Consequences; Kin Selection; Kinship, Evolution of; Marriage Systems, Evolution of; Sociobiology: Overview.

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