In the terrible days after the terrorist attacks of September 11, 2001, I felt an urge so primitive I was embarrassed to admit it to my friends: I wanted to put an American flag decal on my car.

The urge seemed to come out of nowhere, with no connection to anything I’d ever done. It was as if there was an ancient alarm box in the back of my brain with a sign on it that said, “In case of foreign attack, break glass and push button.” I hadn’t known the alarm box was there, but when those four planes broke the glass and pushed the button I had an overwhelming sense of being an American. I wanted to do something, anything, to support my team. Like so many others, I gave blood and donated money to the Red Cross. I was more open and helpful to strangers. And I wanted to display my team membership by showing the flag in some way.

But I was a professor, and professors don’t do such things. Flag waving and nationalism are for conservatives. Professors are liberal globetrotting universalists, reflexively wary of saying that their nation is better than other nations. When you see an American flag on a car in a UVA staff parking lot, you can bet the car belongs to a secretary or blue-collar worker.

After three days and a welter of feelings I’d never felt before, I found a solution to my dilemma. I put an American flag in one corner of my rear windshield, and I put the United Nations flag in the opposite corner. That way I could announce that I loved my country, but don’t worry, folks, I don’t place it above other countries, and this was, after all, an attack on the whole world, sort of, right?

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1 In the social sciences and humanities, conservatives went from being merely underrepresented in the decades after World War II to being nearly extinct by the 1990s except in economics. One of the main causes of this change was that professors from the “greatest generation,” which fought WWII and was not so highly polarized, were gradually replaced by more politically polarized baby boomers beginning in the 1980s (Rothman, Lichter, and Nevitte 2005).
So far in this book I’ve painted a portrait of human nature that is somewhat cynical. I’ve argued that Glaucon was right and that we care more about looking good than about truly being good.\(^2\) Intuitions come first, strategic reasoning second. We lie, cheat, and cut ethical corners quite often when we think we can get away with it, and then we use our moral thinking to manage our reputations and justify ourselves to others. We believe our own post hoc reasoning so thoroughly that we end up self-righteously convinced of our own virtue.

I do believe that you can understand most of moral psychology by viewing it as a form of enlightened self-interest, and if it’s self-interest, then it’s easily explained by Darwinian natural selection working at the level of the individual. Genes are selfish,\(^3\) selfish genes create people with various mental modules, and some of these mental modules make us strategically altruistic, not reliably or universally altruistic. Our righteous minds were shaped by kin selection plus reciprocal altruism augmented by gossip and reputation management. That’s the message of nearly every book on the evolutionary origins of morality, and nothing I’ve said so far contradicts that message.

But in Part III of this book I’m going to show why that portrait is incomplete. Yes, people are often selfish, and a great deal of our moral, political, and religious behavior can be understood as thinly veiled ways of pursuing self-interest. (Just look at the awful hypocrisy of so many politicians and religious leaders.) But it’s also true that people are groupish. We love to join teams, clubs, leagues, and fraternities. We take on group identities and work shoulder to shoulder with strangers toward common goals so enthusiastically that it seems as if our minds were designed for teamwork. I don’t think we can understand morality, politics, or religion until we have a good picture of human groupishness and its origins. We cannot understand conservative morality and the Durkheimian societies I described in the last chapter. But neither can we understand socialism, communism, and the communalism of the left.

Let me be more precise. When I say that human nature is selfish, I mean that our minds contain a variety of mental mechanisms that make us adept at promoting our own interests, in competition with our peers. When I say that human nature is also groupish, I mean that our minds contain a variety of mental mechanisms that make us adept at promoting our group’s interests, in competition with other groups.\(^4\) We are not saints, but we are sometimes good team players.

Stated in this way, the origin of these groupish mechanisms becomes a puzzle. Do we have groupish minds today because groupish individuals long ago outcompeted less groupish individuals within the same group? If so, then this is just standard, bread-and-butter natural selection operating at the level of the individual. And if that’s the case, then this is Glauconian

\(^2\) This is a reference to Glaucon in Plato’s Republic, who asks whether a man would behave well if he owned the ring of Gyges, which makes its wearer invisible and therefore free from concerns about reputation. See chapter 4.

\(^3\) As Dawkins 1976 so memorably put it. Genes can only code for traits that end up making more copies of those genes. Dawkins did not mean that selfish genes make thoroughly selfish people.

\(^4\) Of course we are groupish in the minimal sense that we like groups, we are drawn to groups. Every animal that lives in herds, flocks, or schools is groupish in that sense. I mean to say far more than this. We care about our groups and want to promote our group’s interests, even at some cost to ourselves. This is not usually true about animals that live in herds and flocks (Williams, 1966).
groupishness—we should expect to find that people care about the appearance of loyalty, not the reality.\(^5\) Or do we have groupish mechanisms (such as the rally-round-the-flag reflex) because groups that succeeded in coalescing and cooperating outcompeted groups that couldn’t get it together? If so, then I’m invoking a process known as “group selection,” and group selection was banished as a heresy from scientific circles in the 1970s.\(^6\)

In this chapter I’ll argue that group selection was falsely convicted and unfairly banished. I’ll present four pieces of new evidence that I believe exonerate group selection (in some but not all forms). This new evidence demonstrates the value of thinking about groups as real entities that compete with each other. This new evidence leads us directly to the third and final principle of moral psychology: *Morality binds and blinds.* I will suggest that human nature is mostly selfish, but with a groupish overlay that resulted from the fact that natural selection works at multiple levels simultaneously. Individuals compete with individuals, and that competition rewards selfishness—which includes some forms of strategic cooperation (even criminals can work together to further their own interests).\(^7\) But at the same time, groups compete with groups, and that competition favors groups composed of true team players—those who are willing to cooperate and work for the good of the group, even when they could do better by slacking, cheating, or leaving the group.\(^8\) These two processes pushed human nature in different directions and gave us the strange mix of selfishness and selflessness that we know today.

**Victorious Tribes?**

Here’s an example of one kind of group selection. In a few remarkable pages of *The Descent of Man*, Darwin made the case for group selection, raised the principal objection to it, and then proposed a way around the objection:

> When two tribes of primeval man, living in the same country, came into competition, if (other circumstances being equal) the one tribe included a great number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other, this tribe would succeed better and conquer the other. . . . The advantage which disciplined soldiers have over undisciplined hordes follows chiefly from the confidence which each man feels in his comrades. . . . *Selfish and contentious*

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\(^5\) I don’t doubt that there is a fair bit of Glauconianism going on when people put on displays of patriotism and other forms of group loyalty. I am simply asserting that our team spirit is not purely Glauconian. We sometimes do treat our groups as sacred, and would not betray them even if we could be assured of a large material reward and perfect secrecy for our betrayal.

\(^6\) See Dawkins 1999/1982, and also see Dawkins’s use of the word *heresy* in Dicks 2000.

\(^7\) This is called *mutualism*—when two or more animals cooperate and all of them get some benefit from the interaction. It is not a form of altruism; it is not a puzzle for evolutionary theory. Mutualism may have been extremely important in the early phases of the evolution of humanity’s ultra-sociality; see Baumard, André, and Sperber Unpublished; Tomasello et al. Unpublished.

\(^8\) I will focus on cooperation in this chapter, rather than altruism. But I am most interested in cooperation in these sorts of cases, in which a truly self-interested Glauconian would not cooperate. We might therefore call these focal cases “altruistic cooperation” to distinguish it from the sort of strategic cooperation that is so easy to explain by natural selection acting at the individual level.
people will not cohere, and without coherence nothing can be effected. A tribe rich in the above qualities would spread and be victorious over other tribes.\footnote{Part I, chapter IV, 134, emphasis added. Dawkins 2006 does not consider this to be a case of true group selection because Darwin did not imagine the tribe growing and then splitting into “daughter tribes” the way a beehive splits into daughter hives. But if we add that detail (which is typically true in hunter-gatherer societies that tend to split when they grow larger than around 150 adults), then this would, by all accounts, be an example of group selection. Okasha 2005 calls this kind MLS-2, in contrast to the less demanding MLS-1, which he thinks is more common early in the process of a major transition. More on this below.}

Cohesive tribes began to function like individual organisms, competing with other organisms. The tribes that were more cohesive generally won. Natural selection therefore worked on tribes the same way it works on every other organism.

But in the very next paragraph, Darwin raised the free rider problem, which is still the main objection raised against group selection:

But it may be asked, how within the limits of the same tribe did a large number of members first become endowed with these social and moral qualities, and how was the standard of excellence raised? \textit{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.} He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature.\footnote{Descent of Man, chapter 5, p. 135, emphasis added. The free rider problem is the \textit{only} objection that Dawkins raises against group selection in The God Delusion, chapter 5.}

Darwin grasped the basic logic of what is now known as \textit{multilevel selection}.$^{11}$ Life is a hierarchy of nested levels, like Russian dolls: genes within chromosomes within cells within individual organisms within hives, societies, and other groups. There can be competition at any level of the hierarchy, but for our purposes (studying morality) the only two levels that matter are those of the individual organism and the group. When groups compete, the cohesive, cooperative group usually wins. But within each group, selfish individuals (free riders) come out ahead. They share in the group’s gains while contributing little to its efforts. The bravest army wins, but within the bravest army, the few cowards who hang back are the most likely of all to survive the fight, go home alive, and become fathers.

Multilevel selection refers to a way of quantifying how strong the selection pressure is at each level, which means how strongly the competition of life favors genes for particular traits.$^{12}$

\footnote{Price 1972.}
\footnote{I note that the old idea that there were genes “for” traits has fared poorly in the genomic age. There are not single genes, or even groups of dozens of genes, that can explain much of the variance in any psychological trait. Yet somehow, nearly every psychological trait is heritable. I will sometimes speak of a gene “for” a trait, but this is just a convenience. What I really mean is that the genome as a whole codes for certain traits, and natural selection alters the genome so that it codes for different traits.}
A gene for suicidal self-sacrifice would be favored by group-level selection (it would help the team win), but it would be so strongly opposed by selection at the individual level that such a trait could only evolve in species such as bees, where competition within the hive has been nearly eliminated and nearly all selection is group selection.\(^{13}\) Bees (and ants and termites) are the ultimate team players: one for all, all for one, all the time,\(^ {14}\) even if that means dying to protect the hive from invaders. (Humans can be turned into suicide bombers, but it takes a great deal of training, pressure, and psychological manipulation. It doesn’t come naturally to us.\(^ {15}\)

Once human groups had some minimal ability to band together and compete with other groups, then group-level selection came into play and the most groupish groups had an advantage over groups of selfish individualists. But how did early humans get those groupish abilities in the first place? Darwin proposed a series of “probable steps” by which humans evolved to the point where there could be groups of team players in the first place.

The first step was the “social instincts.” In ancient times, loners were more likely to get picked off by predators than were their more gregarious siblings, who felt a strong need to stay close to the group. The second step was reciprocity. People who helped others were more likely to get help when they needed it most.

But the most important “stimulus to the development of the social virtues” was the fact that people are passionately concerned with “the praise and blame of our fellow-men.”\(^ {16}\) Darwin, writing in Victorian England, shared Glaucon’s view (from aristocratic Athens) that people are obsessed with their reputations. Darwin believed that the emotions that drive this obsession were acquired by natural selection acting at the individual level: those who lacked a sense of shame or a love of glory were less likely to attract friends and mates. Darwin also added a final step: the capacity to treat duties and principles as sacred, which he saw as part of our religious nature.

When you put these steps together, they take you along an evolutionary path from earlier primates to humans among whom free riding is no longer so attractive. In a real army, which sacralizes honor, loyalty, and country, the coward is not the most likely to make it home and father children. He’s the most likely to get beaten up, left behind, or shot in the back for committing sacrilege. And if he does make it home alive, his reputation will repel women and

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\(^{13}\) I emphasize that group selection or colony-level selection as I have described it here is perfectly compatible with inclusive fitness theory (Hamilton 1964) and with Dawkins’s “selfish gene” perspective. But people who work with bees, ants, and other highly social creatures sometimes say that multilevel selection helps them see phenomena that are less visible when they take the gene’s-eye view; see Seeley 1997.

\(^{14}\) I’m oversimplifying here; species of bees, ants, wasps, and termites vary in the degree to which they have achieved the status of superorganisms. Self-interest is rarely reduced to absolute zero, particularly in bees and wasps, which retain the ability to breed under some circumstances. See Hölldobler and Wilson 2009.

\(^{15}\) I thank Steven Pinker for pointing this out to me in a critique of an early draft of this chapter. Pinker noted that war in pre-state societies is nothing like our modern image of men marching off to die for a cause. There’s a lot of posturing, a lot of Glauconian behavior going on as warriors strive to burnish their reputations. Suicide terrorism occurs only rarely in human history; see Pape 2005, who notes that they occur almost exclusively in situations where a group is defending its sacred homeland from culturally alien invaders. See also Atran 2010 on the role of sacred values in suicide terrorism.

\(^{16}\) Descent of Man, chapter 5, p. 135.
potential employers. Real armies, like most effective groups, have many ways of suppressing selfishness. And anytime a group finds a way to suppress selfishness, it changes the balance of forces in a multilevel analysis: individual-level selection becomes less important, and group-level selection becomes more powerful. For example, if there is a genetic basis for feelings of loyalty and sanctity (i.e., the Loyalty and Sanctity foundations), then intense intergroup competition will make these genes become more common in the next generation. The reason is that groups in which these traits are common will replace groups in which they are rare, even if these genes impose a small cost on their bearers (relative to those that lack them within each group).

In what might be the pithiest and most prescient statement in the history of moral psychology, Darwin summarized the evolutionary origin of morality in this way:

Ultimately our moral sense or conscience becomes a highly complex sentiment—originating in the social instincts, largely guided by the approbation of our fellow-men, ruled by reason, self-interest, and in later times by deep religious feelings, and confirmed by instruction and habit.  

Darwin’s response to the free rider problem satisfied readers for nearly a hundred years, and group selection became a standard part of evolutionary thinking. Unfortunately, most writers did not bother to work out exactly how each particular species solved the free rider problem, as Darwin had done for human beings. Claims about animals behaving “for the good of the group” proliferated—for example, the claim that individual animals restrain their grazing or their breeding so as not to put the group at risk of overexploiting its food supply. Even more lofty claims were made about animals acting for the good of the species, or even of the ecosystem. These claims were naive because individuals that followed the selfless strategy would leave fewer surviving offspring and would soon be replaced in the population by the descendants of free riders.

In 1966, this loose thinking was brought to a halt, along with almost all thinking about group selection.

A Fast Herd of Deer?
In 1955, a young biologist named George Williams attended a lecture at the University of Chicago by a termite specialist. The speaker claimed that many animals are cooperative and helpful, just like termites. He said that old age and death are the way that nature makes room for the younger and fitter members of each species. But Williams was well versed in genetics and evolution, and he was repulsed by the speaker’s Panglossian mushiness. He saw that animals are

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17 See in particular Miller 2007, on how sexual selection contributed to the evolution of morality. People go to great lengths to advertise their virtues to potential mates.
18 Descent of Man, Part I, chapter 5, 137. See Richerson and Boyd 2004, who make the case that Darwin basically got it right.
19 A main target of Williams’s ire was Wynne-Edwards 1962.
not going to die to benefit others, except in very special circumstances such as those that prevail in a termite nest (where all are sisters). He set out to write a book that would “purge biology” of such sloppy thinking once and for all.20

In *Adaptation and Natural Selection* (published in 1966), Williams told biologists how to think clearly about adaptation. He saw natural selection as a design process. There’s no conscious or intelligent designer, but Williams found the language of design useful nonetheless.21 For example, wings can only be understood as biological mechanisms designed to produce flight. Williams noted that adaptation at a given level always implies a selection (design) process operating at that level, and he warned readers not to look to higher levels (such as groups) when selection effects at lower levels (such as individuals) can fully explain the trait.

He worked through the example of running speed in deer. When deer run in a herd, we observe a fast herd of deer, moving as a unit and sometimes changing course as a unit. We might be tempted to explain the herd’s behavior by appealing to group selection: for millions of years, faster herds have escaped predators better than slower herds, and so over time fast herds replaced slower herds. But Williams pointed out that deer have been exquisitely well designed as individuals to flee from predators. The selection process operated at the level of individuals: slower deer got eaten, while their faster cousins in the same herd escaped. There is no need to bring in selection at the level of the herd. A fast herd of deer is nothing more than a herd of fast deer.22

Williams gave an example of what it would take to force us up to a group-level analysis: behavioral mechanisms whose goal or function was clearly the protection of the group, rather than the individual. If deer with particularly keen senses served as sentinels, while the fastest runners in the herd tried to lure predators away from the herd, we’d have evidence of group-related adaptations, and, as Williams put it, “only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations.”23

Williams said that group selection was possible in theory. But then he devoted most of the book to proving his thesis that “group-related adaptations do not in fact exist.”24 He gave examples from across the animal kingdom, showing in every case that what looks like altruism or self-sacrifice to a naive biologist (such as that termite specialist) turns out to be either individual selfishness or kin selection (whereby costly actions make sense because they benefit other copies of the same genes in closely related individuals, as happens with termites). Richard Dawkins did the same thing in his 1976 best seller *The Selfish Gene*, granting that group selection is possible but then debunking apparent cases of group-related adaptations. By the late 1970s there was a strong consensus that anyone who said that a behavior occurred “for the good of the group” was a fool who could be safely ignored.

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20 Williams 1966, p. 4.
21 Williams (ibid., pp. 8–9) defined an adaptation as a biological mechanism that produces at least one effect that can properly be called its goal.
22 Williams wrote about a “fleet herd of deer,” but I have substituted in the word *fast* for the less common word *fleet*.
23 Ibid., pp. 92–93.
24 Ibid., p. 93.
We sometimes look back on the 1970s as the “me decade.” That term was first applied to the growing individualism of American society, but it describes a broad set of changes in the social sciences as well. The idea of people as *Homo economicus* spread far and wide. In social psychology, for example, the leading explanation of fairness (known as “equity theory”) was based on four axioms, the first of which was “Individuals will try to maximize their outcomes.” The authors then noted that “even the most contentious scientist would find it difficult to challenge our first proposition. Theories in a wide variety of disciplines rest on the assumption that ‘man is selfish.’” All acts of apparent altruism, cooperation, and even simple fairness had to be explained, ultimately, as covert forms of self-interest.

Of course, real life is full of cases that violate the axiom. People leave tips in restaurants they’ll never return to; they donate anonymously to charities; they sometimes drown after jumping into rivers to save children who are not their own. No problem, said the cynics; these are just misfirings of ancient systems designed for life in the small groups of the Pleistocene, where most people were close kin. Now that we live in large anonymous societies, our ancient selfish circuits erroneously lead us to help strangers who will not help us in return. Our “moral qualities” are not adaptations, as Darwin had believed. They are by-products; they are mistakes. Morality, said Williams, is “an accidental capability produced, in its boundless stupidity, by a biological process that is normally opposed to the expression of such a capability.” Dawkins shared this cynicism: “Let us try to teach generosity and altruism because we are born selfish.”

I disagree. Human beings are the giraffes of altruism. We’re one-of-a-kind freaks of nature who occasionally—even if rarely—can be as selfless and team-spirited as bees. If your moral ideal is the person who devotes her life to helping strangers, well then, OK—such people are so rare that we send film crews out to record them for the evening news. But if you focus, as

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26 I agree that genes are always “selfish,” and all parties to these debates agree that selfish genes can make strategically generous people. The debate is over whether human nature includes any mental mechanisms that make people put the good of the group ahead of their own interests, and if so, whether such mechanisms count as group-level adaptations.
27 This turns out not to be true. In a survey of thirty-two hunter-gatherer societies, Hill et al. 2011 found that for any target individual, only about 10 percent of his or her fellow group mates were close kin. The majority had no blood relationship. Hamilton’s coefficient of genetic relatedness among the Ache was a mere 0.054. This is a problem for theories that try to explain human cooperation by kin selection.
29 Dawkins 1976, p. 3. In his introduction to the thirtieth-anniversary edition, Dawkins regrets his choice of words, because selfish genes can and do cooperate with each other, and they can and do make vehicles such as people who can cooperate with each other. But his current views still seem incompatible with the sort of groupishness and team-spiritedness that I describe in this chapter and the next.
30 Primatologists have long reported acts that appear to be altruistic during their observations of unconstrained interactions in several primate species, but until recently nobody was able to show altruism in a controlled lab setting in the chimpanzee. There is now one study – Horner et al. 2011 – showing that chimps will choose the option that brings greater benefit to a partner at no cost to themselves. Chimps are aware that they can produce a benefit, and they choose to do so. But because this choice imposes no cost on the chooser, it fails to meet many definitions of altruism. I believe the anecdotes about chimp altruism, but I stand by my claim that humans are the “giraffes” of altruism. Even if chimps and other primates can do it a little bit, we do it vastly more.
Darwin did, on behavior in groups of people who know each other and share goals and values, then our ability to work together, divide labor, help each other, and function as a team is so all-pervasive that we don’t even notice it. You’ll never see the headline “Forty-five Unrelated College Students Work Together Cooperatively, and for No Pay, to Prepare for Opening Night of Romeo and Juliet.”

When Williams proposed his fanciful example of deer dividing labor and working together to protect the herd, was it not obvious that human groups do exactly that? By his own criterion, if people in every society readily organize themselves into cooperative groups with a clear division of labor, then this ability is an excellent candidate for being a group-related adaptation. As Williams himself put it: “Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations.”

The 9/11 attacks activated several of these group-related adaptations in my mind. The attacks turned me into a team player, with a powerful and unexpected urge to display my team’s flag and then do things to support the team, such as giving blood, donating money, and, yes, supporting the leader. And my response was tepid compared to the hundreds of Americans who got in their cars that afternoon and drove great distances to New York in the vain hope that they could help to dig survivors out of the wreckage, or the thousands of young people who volunteered for military service in the following weeks. Were these people acting on selfish motives, or groupish motives?

The rally-round-the-flag reflex is just one example of a groupish mechanism. It is exactly the sort of mental mechanism you’d expect to find if we humans were shaped by group selection in the way that Darwin described. I can’t be certain, however, that this reflex really did evolve by group-level selection. Group selection is controversial among evolutionary theorists, most of whom still agree with Williams that group selection never actually happened among humans. They think that anything that looks like a group-related adaptation will—if you look closely enough—turn out to be an adaptation for helping individuals outcompete their neighbors within the same group, not an adaptation for helping groups outcompete other groups.

Before we can move on with our exploration of morality, politics, and religion, we’ve got to address this problem. If the experts are divided, then why should we side with those who believe that morality is (in part) a group-related adaptation?

31 I did not like George W. Bush at any point during his presidency, but I did trust that his vigorous response to the attacks, including the U.S. invasion of Afghanistan, was the right one. Of course, leaders can easily exploit the rally-around-the-flag response for their own ends, as many believe happened with the subsequent invasion of Iraq. See Clarke 2004.

32 The reflex doesn’t require a flag; it refers to the reflex to come together and show signs of group solidarity in response to an external threat. For reviews of the literature on this effect, see Dion 1979; Kesebir, forthcoming.

In the following sections I’ll give you four reasons. I’ll show you four “exhibits” in my defense of multilevel selection (including group selection). But my goal here is not just to build a legal case in an academic battle that you might care nothing about. My hope in these exhibits is to show you that morality is the key to understanding humanity. I’ll take you on a brief tour of humanity’s origins in which we’ll see how groupishness helped us transcend selfishness. I’ll show that our groupishness—despite all of the ugly and tribal things it makes us do—is one of the magic ingredients that made it possible for civilizations to burst forth, cover the Earth, and live ever more peacefully in just a few thousand years.\(^{34}\)

**Exhibit A: Major Transitions in Evolution**

Suppose you entered a boat race. One hundred rowers, each in a separate rowboat, set out on a ten-mile race along a wide and slow-moving river. The first to cross the finish line will win $10,000. Halfway into the race, you’re in the lead. But then, from out of nowhere, you’re passed by a boat with two rowers, each pulling just one oar. No fair! Two rowers joined together into one boat! And then, stranger still, you watch as that rowboat is overtaken by a train of three such rowboats, all tied together to form a single long boat. The rowers are identical septuplets. Six of them row in perfect synchrony while the seventh is the coxswain, steering the boat and calling out the beat for the rowers. But at least those cheaters are deprived of victory just before they cross the finish line, for they in turn are passed by an enterprising group of twenty-four sisters who rented a motorboat. It turns out that there are no rules in this race about what kind of vehicles are allowed.

That was a metaphorical history of life on Earth. For the first billion years of life or so, the only organisms were prokaryotic cells (such as bacteria). Each was a solo operation, competing with others and reproducing copies of itself.

But then, around 2 billion years ago, two bacteria somehow joined together inside a single membrane, which explains why mitochondria have their own DNA, unrelated to the DNA in the nucleus.\(^{35}\) These are the two-person rowboats in my example. Cells that had internal organelles could reap the benefits of cooperation and the division of labor (see Adam Smith). There was no longer any competition between these organelles, for they could reproduce only when the entire cell reproduced, so it was “one for all, all for one.” Life on Earth underwent what biologists call a “major transition.”\(^{36}\) Natural selection went on as it always had, but now there was a radically new kind of creature to be selected. There was a new kind of *vehicle* by which selfish genes could replicate themselves. Single-celled eukaryotes were wildly successful and spread throughout the oceans.

\(^{34}\) Racism, genocide, and suicide bombing are all manifestations of groupishness. They are not things that people do in order to outcompete their local peers; they are things people do to help their groups outcompete other groups. For evidence that rates of violence are vastly lower in civilized societies than among hunter-gatherers, see Pinker 2011. Pinker explains how increasingly strong states plus the spread of capitalism have led to ever-decreasing levels of violence, even when you include the wars and genocides of the twentieth century. (The trend is not perfectly linear—individual nations can experience some regressions. But the overall trend of violence is steadily downward.)\(^{35}\) Margulis 1970. In plant cells, chloroplasts also have their own DNA.\(^{36}\) Maynard Smith and Szathmary 1997; Bourke 2011.
A few hundred million years later, some of these eukaryotes developed a novel adaptation: they stayed together after cell division to form multicellular organisms in which every cell had exactly the same genes. These are the three-boat septuplets in my example. Once again, competition is suppressed (because each cell can only reproduce if the organism reproduces, via its sperm or egg cells). A group of cells becomes an individual, able to divide labor among the cells (which specialize into limbs and organs). A powerful new kind of vehicle appears, and in a short span of time the world is covered with plants, animals, and fungi. It’s another major transition.

Major transitions are rare. The biologists John Maynard Smith and Eors Szathmary count just eight clear examples over the last 4 billion years (the last of which is human societies). But these transitions are among the most important events in biological history, and they are examples of multilevel selection at work. It’s the same story over and over again: Whenever a way is found to suppress free riding so that individual units can cooperate, work as a team, and divide labor, selection at the lower level becomes less important, selection at the higher level becomes more powerful, and that higher-level selection favors the most cohesive superorganisms. (A superorganism is an organism made out of smaller organisms.) As these superorganisms proliferate, they begin to compete with each other, and to evolve for greater success in that competition. This competition among superorganisms is one form of group selection. There is variation among the groups, and the fittest groups pass on their traits to future generations of groups.

\[37\] There is an important flaw in my “boat race” analogy: the new vehicles don’t really “win” the race. Prokaryotes are still quite successful; they still represent most of the life on earth by weight and by number. But still, new vehicles seem to come out of nowhere and then claim a substantial portion of the earth’s available bio-energy.

\[38\] Maynard Smith and Szathmary attribute the human transition to language, and suggest that the transition occurred around 40,000 years ago. Bourke 2011 offers an up-to-date discussion. He identifies six major kinds of transitions, and notes that several of them have occurred dozens of times independently, e.g., the transition to eusociality.

\[39\] Hölldobler and Wilson 2009. Many theorists prefer terms other than superorganism. Bourke 2011, for example, calls them simply “individuals.”

\[40\] Okasha 2006 calls this MLS-2. I’ll call it selection among stable groups in contrast to MLS-1, which I’ll call selection among shifting groups. This is a subtle distinction that is crucial in discussions among specialists who debate whether group selection has actually occurred. It is too subtle to explain in the main text, but the general idea is this: For selection among stable groups, we focus on the group as an entity, and we track its fitness as it competes with other groups. For this kind of selection to matter, groups must maintain strong boundaries with a high degree of genetic relatedness inside each group over many generations. Hunter-gatherer groups as we know them today do not do this; individuals come and go, through marriage or for other reasons. (Although, as I point out below, the ways of current hunter-gatherers cannot be taken to be the ways that our ancestors lived 100,000 years ago, or even 30,000 years ago.) In contrast, for selection among shifting groups to affect gene frequencies, all that is needed is that the social environment be composed of multiple kinds of groups which compete with each other, perhaps just for a few days or months. We focus not on the fitness of the groups, but on the fitness of individuals who either have, or lack, group-related adaptations. Individuals whose minds contain effective group-related adaptations end up playing on the winning team more often—at least if the population structure is somewhat lumpy or uneven, such that groupish individuals have a better than chance likelihood of finding themselves on the same team. Some critics say that this is not “real” group selection, or that it ends up being the same thing as individual-level selection, but Okasha disagrees. He points out that selection among shifting groups happens early in the process of a major transition, and it leads to adaptations that increase cohesiveness and suppress free riding, which then pave the way for selection among stable groups to operate in the later stages of a major transition. Some have argued that human beings are “stalled” midway
Major transitions may be rare, but when they happen, the Earth often changes. Just look at what happened more than 100 million years ago when some wasps developed the trick of dividing labor between a queen (who lays all the eggs) and several kinds of workers who maintain the nest and bring back food to share. This trick was discovered by the early hymenoptera (members of the order that includes wasps, which gave rise to bees and ants) and it was discovered independently several dozen other times (by the ancestors of termites, naked mole rats, and some species of shrimp, aphids, beetles, and spiders). In each case, the free rider problem was surmounted and selfish genes began to craft relatively selfless group members who together constituted a supremely selfish group.

These groups were a new kind of vehicle: a hive or colony of close genetic relatives, which functioned as a unit (e.g., in foraging and fighting) and reproduced as a unit. These are the motorboating sisters in my example, taking advantage of technological innovations and mechanical engineering that had never before existed. It was another transition. Another kind of group began to function as though it were a single organism, and the genes that got to ride around in colonies crushed the genes that couldn’t “get it together” and rode around in the bodies of more selfish and solitary insects. The colonial insects represent just 2 percent of all insect species, but in a short period of time they claimed the best feeding and breeding sites for themselves, pushed their competitors to marginal grounds, and changed most of the Earth’s terrestrial ecosystems (for example, by enabling the evolution of flowering plants, which need pollinators). Now they’re the majority, by weight, of all insects on Earth.

What about human beings? Since ancient times, people have likened human societies to beehives. But is this just a loose analogy? If you map the queen of the hive onto the queen or king of a city-state, then yes, it’s loose. A hive or colony has no ruler, no boss. The queen is just the ovary. But if we simply ask whether humans went through the same evolutionary process as bees—a major transition from selfish individualism to groupish hives that prosper when they find a way to suppress free riding—then the analogy gets much tighter.

Many animals are social: they live in groups, flocks, or herds. But only a few animals have crossed the threshold and become ultrasocial, which means that they live in very large groups that have some internal structure enabling them to reap the benefits of the division of

through the major transition process (Stearns 2007). I think that’s another way of saying that we are 90 percent chimp and 10 percent bee. For a full explanation of MLS-1 and MLS-2, see Okasha 2006 chapters 2 and 6.

I do not mean to imply that there is an overall or inevitable progression of life toward ever greater complexity and cooperation. Multilevel selection means that there are always antagonistic selection forces operating at different levels. Sometimes species revert from superorganisms to more solitary forms. But a world with bees, ants, wasps, termites, and humans in it has many more tons of cooperative individuals than did the world of 200 million years ago.


Hölldobler and Wilson 2009; E. O. Wilson 1990. I note that the new superorganisms don’t shoot up to dominance right away after the free rider problem is addressed. Superorganisms go through a period of refinement until they begin to take maximum advantage of their new cooperation, which gets improved by group-level selection as they compete with other superorganisms. The eusocial hymenoptera first emerged more than 100 million years ago, but they didn’t shoot up to world domination until closer to 50 million years ago. Same story, perhaps, for humans, who probably developed fully groupish minds in the late Pleistocene, but didn’t shoot up to world domination until the late Holocene.
Beehives and ant nests, with their separate castes of soldiers, scouts, and nursery attendants, are examples of ultrasociality, and so are human societies.

One of the key features that has helped all the nonhuman ultrasocials to cross over appears to be the need to defend a shared nest. Biologists Ernst Hölldobler and E. O. Wilson summarize the recent finding that ultrasociality (also called “eusociality”45) is found among a few species of shrimp, aphids, thrips, and beetles, as well as among wasps, bees, ants, and termites.

In all the known [species that] display the earliest stages of eusociality, their behavior protects a persistent, defensible resource from predators, parasites, or competitors. The resource is invariably a nest plus dependable food within foraging range of the nest inhabitants.46

Hölldobler and Wilson give supporting roles to two other factors: the need to feed offspring over an extended period (which gives an advantage to species that can recruit siblings or males to help out Mom) and intergroup conflict. All three of these factors applied to those first early wasps camped out together in defensible naturally occurring nests (such as holes in trees). From that point on, the most cooperative groups got to keep the best nesting sites, which they then modified in increasingly elaborate ways to make themselves even more productive and more protected. Their descendants include the honeybees we know today, whose hives have been described as “a factory inside a fortress.”47

Those same three factors applied to human beings. Like bees, our ancestors were (1) territorial creatures with a fondness for defensible nests (such as caves) who (2) gave birth to needy offspring that required enormous amounts of care, which had to be given while (3) the group was under threat from neighboring groups. For hundreds of thousands of years, therefore, conditions were in place that pulled for the evolution of ultrasociality, and as a result, we are the only ultrasocial primate. The human lineage may have started off acting very much like chimps,48 but by the time our ancestors started walking out of Africa, they had become at least a little bit like bees.
And much later, when some groups began planting crops and orchards, and then building granaries, storage sheds, fenced pastures, and permanent homes, they had an even steadier food supply that had to be defended even more vigorously. Like bees, humans began building ever more elaborate nests, and in just a few thousand years, a new kind of vehicle appeared on Earth—the city-state, able to raise walls and armies.\textsuperscript{49} City-states and later empires spread rapidly across Eurasia, North Africa, and Mesoamerica, changing many of the Earth’s ecosystems and allowing the total tonnage of human beings to shoot up from insignificance at the start of the Holocene (around 12,000 years ago) to world domination today.\textsuperscript{50} As the colonial insects did to the other insects, we have pushed all other mammals to the margins, to extinction, or to servitude. The analogy to bees is not shallow or loose. Despite their many differences, human civilizations and beehives are both products of major transitions in evolutionary history. They are motorboats.

The discovery of major transitions is exhibit A in the retrial of group selection. Group selection may or may not be common among other animals, but it happens whenever individuals find ways to suppress selfishness and work as a team, in competition with other teams.\textsuperscript{51} Group selection creates group-related adaptations. It is not farfetched, and it should not be a heresy to suggest that this is how we got the groupish overlay that makes up part of our righteous minds.

\textit{Exhibit B: Shared Intentionality}

In 49 BCE, Gaius Julius made the momentous decision to cross the Rubicon, a shallow river in northern Italy. He broke Roman law (which forbade generals from approaching Rome with their armies), started a civil war, and became Julius Caesar, the absolute ruler of Rome. He also gave us a metaphor for any small action that sets in motion an unstoppable train of events with momentous consequences.

It’s great fun to look back at history and identify Rubicon crossings. I used to believe that there were too many small steps in the evolution of morality to identify one as the Rubicon, but I changed my mind when I heard Michael Tomasello, one of the world’s foremost experts on chimpanzee cognition, utter this sentence: “It is inconceivable that you would ever see two chimpanzees carrying a log together.”\textsuperscript{52}

\textsuperscript{49} I am not saying that human brains or genes changed radically at this time. I follow Richerson and Boyd 2005, and Tooby and Cosmides 1992 in assuming that most of the genes that made life in city-states possible were shaped during hundreds of thousands of years of hunter-gatherer life. But as I’ll say below, I think it’s likely that there was some additional genetic evolution during the Holocene.

\textsuperscript{50} We’re not literally a majority of the world’s mammalian weight, but that’s only because we raise so many cows, pigs, sheep, and dogs. If you include us together with our domesticated servants, our civilizations now account for an astonishing 98 percent of all mammal life, by weight according to a statement by Donald Johanson, made at a conference on “Origins” at Arizona State University in April 2009.

\textsuperscript{51} Critics of group selection add the criterion that the groups must reproduce themselves, including “budding off” to form multiple new groups that closely resemble the original group. This is true for MLS-2 (selection among stable groups), but is not necessary for MLS-1 (selection among shifting groups); see Okasha 2006, and see note 40 above.

\textsuperscript{52} Tomasello gave three major lectures at UVA in October 2010. His basic argument, including a quote like this one, can be found in Tomasello et al. 2005. Chimpanzees can recruit a collaborator to help them get food in a task that requires two chimps to get any food (Melis, Hare, and Tomasello 2006) but they don’t seem to be sharing intentions or truly coordinating with that collaborator.
I was stunned. Chimps are arguably the second-smartest species on the planet, able to make tools, learn sign language, predict the intentions of other chimps, and deceive each other to get what they want. As individuals, they’re brilliant. So why can’t they work together? What are they missing?

Tomasello’s great innovation was to create a set of simple tasks that could be given to chimps and to human toddlers in nearly identical form.\(^{53}\) Solving the task earned the chimp or child a treat (usually a piece of food for the chimp, a small toy for the child). Some of the tasks required thinking only about physical objects in physical space—for example, using a stick to pull in a treat that was out of reach, or choosing the dish that had the larger number of treats in it rather than the smaller number. Across all ten tasks, the chimps and the two-year-olds did equally well, solving the problems correctly about 68 percent of the time.

But other tasks required collaborating with the experimenter, or at least recognizing that she intended to share information. For example, in one task, the experimenter demonstrated how to remove a treat from a clear tube by poking a hole in the paper that covered one end, and then she gave an identical tube to the chimp or child. Would the subjects understand that the experimenter was trying to teach them what to do? In another task, the experimenter hid the treat under one of two cups and then tried to show the chimp or child the correct cup (by looking at it or pointing to it). The kids aced these social challenges, solving them correctly 74 percent of the time. The chimps bombed, solving them just 35 percent of the time (no better than chance on many of the tasks).

According to Tomasello, human cognition veered away from that of other primates when our ancestors developed *shared intentionality*.\(^{54}\) At some point in the last million years, a small group of our ancestors developed the ability to share mental representations of tasks that two or more of them were pursuing together. For example, while foraging, one person pulls down a branch while the other plucks the fruit, and they both share the meal. Chimps never do this. Or while hunting, the pair splits up to approach an animal from both sides. Chimps sometimes appear to do this, as in the widely reported cases of chimps hunting colobus monkeys,\(^{55}\) but Tomasello argues that the chimps are not really working together. Rather, each chimp is surveying the scene and then taking the action that seems best to him at that moment.\(^{56}\) Tomasello notes that these monkey hunts are the *only* time that chimps seem to be working together, yet even in these rare cases they fail to show the signs of real cooperation. They make

\(^{53}\) Herrmann et al. 2007. The full descriptions of the tasks, including videos, can be downloaded at http://www.sciencemag.org/content/317/5843/1360/suppl/DC1, but note that the videos always show chimps solving the tasks, even though they rarely did so on the social tasks. Note also that the experiment included a third group—orangutans, who fared worse than the chimps at both kinds of tasks.

\(^{54}\) Tomasello et al. 2005. Tomasello cites earlier work by autism researcher Simon Baron-Cohen (1995) who had described a “shared attention mechanism” that develops in normal children, but not in children with autism, which leaves them “mind-blind.”

\(^{55}\) Boesch 1994.

\(^{56}\) Tomasello et al., forthcoming. It is clear that chimps form political coalitions—two males will team up to oppose the current alpha male, as documented by de Waal 1982. But the *coordination* here is weak at best. They don’t work together on any particular task or challenge; they just groom each other and don’t fight each other while one or both of them challenge the alpha.
no effort to communicate with each other, for example, and they are terrible at sharing the spoils among the hunters, each of whom must use force to obtain a share of meat at the end. They all chase the monkey at the same time, yet they don’t all seem to be on the same page about the hunt.

In contrast, when early humans began to share intentions, their ability to hunt, gather, raise children, and raid their neighbors increased exponentially. Everyone on the team now had a mental representation of the task, knew that his or her partners shared the same representation, knew when a partner had acted in a way that impeded success or that hogged the spoils, and reacted negatively to such violations. When everyone in a group began to share a common understanding of how things were supposed to be done, and then felt a flash of negativity when any individual violated those expectations, the first moral matrix was born.57 (Remember that a matrix is a consensual hallucination.) That, I believe, was our Rubicon crossing.

Tomasello believes that human ultrasociality arose in two steps. The first was the ability to share intentions in groups of two or three people who were actively hunting or foraging together. (That was the Rubicon.) Then, after several hundred thousand years of evolution for better sharing and collaboration as nomadic hunter-gatherers, more collaborative groups began to get larger, perhaps in response to the threat of other groups. Victory went to the most cohesive groups—the ones that could scale up their ability to share intentions from three people to three hundred or three thousand people. This was the second step: natural selection favored increasing levels of what Tomasello calls “group-mindedness”—the ability to learn and conform to social norms, feel and share group-related emotions, and ultimately, to create and obey social institutions, including religion. A new set of selection pressures operated within groups (e.g., nonconformists were punished, or at very least were less likely to be chosen as partners for joint ventures58) as well as between groups (cohesive groups took territory and other resources from less cohesive groups).

Shared intentionality is exhibit B in the retrial of group selection. Once you grasp Tomasello’s deep insight, you begin to see the vast webs of shared intentionality out of which human groups are constructed. Many people assume that language was our Rubicon, but language became possible only after our ancestors got shared intentionality. Tomasello notes that a word is not a relationship between a sound and an object. It is an agreement among people who share a joint representation of the things in their world, and who share a set of conventions for

57 De Waal 1996 argues that chimpanzee communities develop norms and administer punishment to norm violators. However, examples of such norms among chimps are rare, and chimps certainly don’t build up increasingly elaborate networks of norms over time. As with so much else about chimps, such as their cultural abilities, they seem to have many of the “building blocks” of human morality, but they don’t seem to put them together to build moral systems.

58 A major topic of debate in evolutionary circles is why any individual would pay the costs of punishing other, which might include a violent reaction from the individual being punished. But if the punishment is very low-cost, e.g., gossiping, or simply not choosing the transgressor for joint ventures (Baumard, André, and Sperber unpublished), then the cost becomes quite small, and computer models show various ways in which a tendency to punish could emerge; see Panchanathan and Boyd 2004. As the cost of free riding increases and it becomes increasingly rare, group-level selection on many other traits becomes increasingly powerful, compared to individual-level selection.
communicating with each other about those things. If the key to group selection is a shared defensible nest, then shared intentionality allowed humans to construct nests that were vast and ornate yet weightless and portable. Bees construct hives out of wax and wood fibers, which they then fight, kill, and die to defend. Humans construct moral communities out of shared norms, institutions, and gods that, even in the twenty-first century, they fight, kill, and die to defend.

Exhibit C: Genes and Cultures Coevolve
When did our ancestors cross the Rubicon? We’ll never know when the first pair of foragers worked as a team to pluck figs from a tree, but when we begin to see signs in the fossil record of cultural innovations accumulating and building on earlier innovations, we can guess that the innovators had crossed over. When culture accumulates, it means that people are learning from each other, adding their own innovations, and then passing their ideas on to later generations.

Our ancestors first began to diverge from the common ancestor we share with chimps and bonobos between 5 million and 7 million years ago. For the next few million years, there were many species of hominids walking around on two legs in Africa. But judging from their brain size and their limited use of tools, these creatures (including australopithecines such as Lucy) are better thought of as bipedal apes than as early humans.

Then, beginning around 2.4 million years ago, hominids with larger brains begin to appear in the fossil record. These were the first members of the genus Homo, including Homo habilis, so named because these creatures were “handy men” compared to their ancestors. They left behind a profusion of simple stone tools known as the Oldowan tool kit. These tools, mostly just sharp flakes they had knocked off larger stones, helped Homo habilis to cut and scrape meat off carcasses killed by other animals. Homo habilis was not much of a hunter.

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59 For more on cumulative culture and gene-culture coevolution, see Richerson and Boyd’s masterpiece Not by Genes Alone. I am heavily indebted to them for many ideas in this chapter.
60 It is likely that these creatures made some tools. Even chimpanzees make some tools. But there’s not much evidence of tool use in the fossil record until the end of this period, nearing the emergence of the genus Homo.
Then, beginning around 1.8 million years ago, some hominids in East Africa began making new and more finely crafted tools, known as the Acheul tool kit. The main tool was a teardrop-shaped hand axe, and its symmetry and careful crafting jumps out at us as something new under the sun, something made by minds like ours (see Figure 9.2). This seems like a promising place to start talking about cumulative culture. But here’s the weird thing: Acheul tools are nearly identical everywhere, from Africa to Europe to Asia, for more than a million years. There’s hardly any variation, which suggests that the knowledge of how to make these tools may not have been passed on culturally. Rather, the knowledge of how to make these tools may have become innate, just as the “knowledge” of how to build a dam is innate in beavers.

Figure 9.1. *Timeline of major events in human evolution.*

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61 Dates drawn from Potts and Sloan, 2010; Richerson and Boyd 2005; and Tattersall, 2009.


63 Richerson and Boyd 2005 make this point. Cultural artifacts almost never show such stability across time and space. Think, for example, about swords and teapots, which fill museum cases because cultures are so inventive in the ways they create objects that fulfill the same basic functions.
Figure 9.2. Acheulean hand axe.

It’s only around 600,000 or 700,000 years ago that we begin to see creatures who may have crossed over. The first hominids with brains as large as ours begin appearing in Africa and then Europe. They are known collectively as *Homo heidelbergensis*, and they were the ancestors of Neanderthals as well as of us. At their campsites we find the first clear evidence of hearths, and of spears. The oldest known spears were just sharpened sticks, but later they become sharp stone points attached to wooden shafts and balanced for accurate throwing. These people made complex weapons and then worked together to hunt and kill large animals, which they brought back to a central campsite to be butchered, cooked, and shared.\(^4\)

*Homo heidelbergensis* is therefore our best candidate for Rubicon crosser.\(^5\) These people had cumulative culture, teamwork, and a division of labor. They must have had shared intentionality, including at least some rudimentary moral matrix that helped them work together and then share the fruits of their labor. By crossing over, they transformed not just the course of human evolution but the very nature of the evolutionary process. From that point onward, people lived in an environment that was increasingly of their own making.

The anthropologists Pete Richerson and Rob Boyd have argued that cultural innovations (such as spears, cooking techniques, and religions) evolve in much the same way that biological innovations evolve,\(^6\) and the two streams of evolution are so intertwined that you can’t study

\(^4\) My account of *Homo heidelbergensis* is drawn from Potts and Sloan 2010 and from Richerson and Boyd 2005, chapter 4.

\(^5\) My account is speculative; it’s always hazardous to guess when a specific event occurred or a specific ability emerged. Tomasello, who is more cautious than I am, has never identified a time or a species in which shared intentionality first emerged. But when I asked him if *Homo heidelbergensis* was the best candidate, he said yes.

\(^6\) There are two major differences: (1) cultural innovations spread laterally, as people see and then copy an innovation; genetic innovations can only spread vertically, from parent to child, and (2) cultural innovations can be driven by intelligent designers—people who are trying to solve a problem; genetic innovation only happens by random mutation. See Richerson and Boyd 2005. Dawkins (1976) first popularized the notion of cultural evolution
one without studying both. For example, one of the best understood cases of gene-culture coevolution occurred among the first people who domesticated cattle. In humans, as in all other mammals, the ability to digest lactose (the sugar in milk) is lost during childhood. The gene that makes lactase (the enzyme that breaks down lactose) shuts off after a few years of service, because mammals don’t drink milk after they are weaned. But those first cattle keepers, in northern Europe and in a few parts of Africa, had a vast new supply of fresh milk, which could be given to their children but not to adults. Any individual whose mutated genes delayed the shutdown of lactase production had an advantage. Over time such people left more milk-drinking descendants than did their lactose-intolerant cousins. (The gene itself has been identified.) Genetic changes then drove cultural innovations as well: groups with the new lactase gene then kept even larger herds, and found more ways to use and process milk, such as turning it into cheese. These cultural innovations then drive further genetic changes, and on and on it goes.

If cultural innovations (such as keeping cattle) can lead to genetic responses (such as adult lactose tolerance), then might cultural innovations related to morality have led to genetic responses as well? Yes. Richerson and Boyd argue that gene-culture coevolution helped to move humanity up from the small-group sociability of other primates to the tribal ultrasociality that is found today in all human societies.

According to their “tribal instincts hypothesis,” human groups have always been in competition to some degree with neighboring groups. The groups that figured out (or stumbled upon) cultural innovations that helped them cooperate and cohere in groups larger than the family tended to win these competitions (just as Darwin said).

Among the most important such innovations is the human love of using symbolic markers to show our group memberships. From the tattoos and face piercings used among Amazonian tribes through the male circumcision required of Jews to the tattoos and facial piercings used by punks in the United Kingdom, human beings take extraordinary, costly, and sometimes painful steps to make their bodies advertise their group memberships. This practice surely started modestly, perhaps just with colored powders for body painting. But however it began, groups that built on it and invented more permanent markers found a way to forge a sense

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67 Tishkoff et al. 2007. Interestingly, it’s a different gene in African populations than in Europeans. The genome is so flexible and adaptive that it often finds multiple ways to respond to a single adaptive pressure.
68 One might argue that modern industrial societies are cosmopolitan and not tribal. But our tendency to form groups within such societies has been linked to the basic social nature of tribalism; see Dunbar 1996. At the other extreme, hunter-gatherers are not just small bands of close kin, as many people suppose. People move in and out of coreiding groups for marriage and for other reasons. Bands maintain close ties of trade and exchange with other bands that are not based on kinship directly, although they may be facilitated by the fact that children of one band so often marry out, joining neighboring bands, while maintaining ties with parents and siblings. Marital exchanges bind groups together, well beyond the individual families involved in the marriage. See Hill et al. 2011.
69 Colored powders and pigments have been found at human campsites dating back as far as 160,000 years ago, and they are thought to have been used for symbolic and ceremonial purposes; see Marean et al. 2007.
of “we” that extended beyond kinship. We trust and cooperate more readily with people who look and sound like us.\textsuperscript{70} We expect them to share our values and norms.

And once some groups developed the \textit{cultural} innovation of prototribalism, they changed the environment within which \textit{genetic} evolution took place. As Richerson and Boyd explain:

Such environments favored the evolution of a suite of new social instincts suited to life in such groups, including a psychology which “expects” life to be structured by moral norms and is designed to learn and internalize such norms; new emotions such as shame and guilt, which increase the chance that the norms are followed, and a psychology which “expects” the social world to be divided into symbolically marked groups.\textsuperscript{71}

In such prototribal societies, individuals who found it harder to play along to restrain their antisocial impulses, and to conform to the most important collective norms would not have been anyone’s top choice when it came time to choose partners for hunting, foraging, or mating. In particular, people who were violent would have been shunned, punished, or in extreme cases killed.

This process has been described as “self-domestication.”\textsuperscript{72} The ancestors of dogs, cats, and pigs got less aggressive as they were domesticated and shaped for partnership with human beings. Only the friendliest ones approached human settlements in the first place; they volunteered to become the ancestors of today’s pets and farm animals.

In a similar way, early humans domesticated themselves when they began to select friends and partners based on their ability to live within the tribe’s moral matrix. In fact, our brains, bodies, and behavior show many of the same signs of domestication that are found in our domestic animals: smaller teeth, smaller body, reduced aggression, and greater playfulness, carried on even into adulthood.\textsuperscript{73} The reason is that domestication generally takes traits that disappear at the end of childhood and keeps them turned on for life. Domesticated animals (including humans) are more childlike, sociable, and gentle than their wild ancestors.

These tribal instincts are a kind of overlay, a set of groupish emotions and mental mechanisms laid down over our older and more selfish primate nature.\textsuperscript{74} It may sound depressing

\textsuperscript{70} Kinzler, Dupoux, and Spelke 2007. See Kesebir forthcoming for a review.
\textsuperscript{71} Richerson and Boyd 2005 p. 214. See also Fessler 2007 on how shame evolved from an emotion of submission to authority into an emotion of conformity to norms.
\textsuperscript{72} Hare, Wobber, and Wrangham, unpublished; Wrangham 2001. Self-domestication (sometimes called autodomestication) is a form of the more general process known as social selection, in which selection results from the choices made by members of one’s own species.
\textsuperscript{73} Hare, Wobber, and Wrangham, Unpublished.
\textsuperscript{74} By saying that our older primate nature is more selfish, I do not mean to contradict Frans de Waal’s work showing the presence of empathy and other building blocks of the human moral sense in chimpanzees and bonobos. I mean only that these building blocks are all easily explained as mechanisms that helped individuals prosper within groups. I don’t think you need group selection to explain chimpanzee nature, but I think you need it to explain human nature. De Waal (2006) criticizes “veneer theorists” who think that morality is a thin veneer covering our true nature, which is selfish. I am not a veneer theorist in that sense. But I am a veneer theorist in suggesting that we humans have some recent adaptations, shaped by group-level selection, that evolved out of our older primate nature but that make us very different from other primates.
to think that our righteous minds are basically tribal minds, but consider the alternative. Our tribal minds make it easy to divide us, but without our long period of tribal living there’d be nothing to divide in the first place. There’d be only small families of foragers—not nearly as sociable as today’s hunter-gatherers—eking out a living and losing most of their members to starvation during every prolonged drought. The coevolution of tribal minds and tribal cultures didn’t just prepare us for war; it also prepared us for far more peaceful coexistence within our groups, and, in modern times, for cooperation on a vast scale as well.

Gene-culture coevolution is Exhibit C in the retrial of group selection. Once our ancestors crossed the Rubicon and became cumulatively cultural creatures, their genes began to coevolve with their cultural innovations. At least some of these innovations were directed at marking members of a moral community, fostering group cohesion, suppressing aggression and free riding within the group, and defending the territory shared by that moral community. These are precisely the sorts of changes that make major transitions happen. Even if group selection played no role in the evolution of any other mammal, human evolution has been so different, since the arrival of shared intentionality and gene-culture coevolution, that humans may well be a special case. The wholesale dismissal of group selection in the 1970s, based mostly on arguments and examples from other species, was premature.

Exhibit D: Evolution Can Be Fast
When exactly did we become ultrasocial? Humans everywhere are so groupish that most of the genetic changes must have been in place before our ancestors spread out from Africa and the Middle East around 50,000 years ago. (I suspect it was the development of cooperative groupishness that enabled these ancestors to conquer the world and take over Neanderthal territory so quickly.) But did gene-culture coevolution stop at that point? Did our genes freeze in place, leaving all later adaptation to be handled by cultural innovation? For decades, many anthropologists and evolutionary theorists said yes. In an interview in 2000, the paleontologist Stephen Jay Gould said that “natural selection has almost become irrelevant in human evolution” because cultural change works “orders of magnitude” faster than genetic change. He next

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75 See Bourke 2011, pp. 3–4.
76 Other than two species of African mole rats, which are the only mammals that qualify as eusocial. The mole rats achieve their eusociality in the same was as bees and ants – by suppressing breeding in all except for a single breeding couple, such that all members of the colony are very close kin. Also, because they dig extensive underground tunnels, they have a shared defensible nest.
77 Some Homo sapiens had left Africa by 70,000 years ago, and were living in and around Israel. During this time there seems to have been some interbreeding with Neanderthals (Green et al. 2010). Some humans may have left Africa between 70,000 and 60,000 years ago and traveled through Yemen and South Asia to become the ancestors of people in New Guinea and Australia. But the group that left Africa and Israel around 50,000 years ago is the group that is believed to have populated Eurasia and the Americas. I therefore use 50,000 years ago as the date for the great dispersion, even though some people had already left in the 20,000 years before that. See Potts and Sloan 2010.
asserted that “there’s been no biological change in humans in 40,000 or 50,000 years. Everything we call culture and civilization we’ve built with the same body and brain.”

If you believe Gould’s assertion that there’s been no biological evolution in the last 50,000 years, then you’ll be most interested in the Pleistocene era (the roughly 2 million years prior to the rise of agriculture), and you’ll dismiss the Holocene (the last 12,000 years) as irrelevant for understanding human evolution. But is 12,000 years really just an eye blink in evolutionary time? Darwin didn’t think so; he wrote frequently about the effects obtained by animal and plant breeders in just a few generations.

The speed at which genetic evolution can occur is best illustrated by an extraordinary study by Dmitri Belyaev, a Soviet scientist who had been demoted in 1948 for his belief in Mendelian genetics. (Soviet morality required the belief that traits acquired during one’s lifetime could be passed on to one’s children.) Belyaev moved to a Siberian research institute, where he decided to test his ideas by conducting a simple breeding experiment with foxes. Rather than selecting foxes based on the quality of their pelts, as fox breeders would normally do, he selected them for tameness. Whichever fox pups were least fearful of humans were bred to create the next generation. Within just a few generations the foxes became tamer. But more important, after nine generations, novel traits began to appear in a few of the pups, and they were largely the same ones that distinguish dogs from wolves. For example, patches of white fur appeared on the head and chest; jaws and teeth shrunk; and tails formerly straight began to curve. After just thirty generations the foxes had become so tame that they could be kept as pets. Lyudmila Trut, a geneticist who had worked with Belyaev on the project and who ran it after his death, described the foxes as “docile, eager to please, and unmistakably domesticated.”

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79 This is known as Lamarckism. Darwin believed it too, erroneously. Lamarckism was helpful to a dictatorship bent on producing a new breed of human being, Soviet Man. Trofim Lysenko was the preferred biologist, rather than Mendel.  
80 Trut 1999.
It’s not just individual-level selection that is fast. A second study done with chickens shows that group selection can produce equally dramatic results. If you want to increase egg output, common sense tells you to breed only the hens that lay the most eggs. But the reality of the egg industry is that hens live crammed together into cages, and the best laying hens tend to be the more aggressive, dominant hens. Therefore, if you use individual selection (breeding only the most productive hens) total productivity actually goes down because aggressive behavior—including killing and cannibalism—goes up.

In the 1980s the geneticist William Muir used group selection to get around this problem.[^1] He worked with cages containing twelve hens each, and he simply picked the cages that produced the most eggs in each generation. Then he bred all of the hens in those cages to produce the next generation. Within just three generations, aggression levels plummeted. By the sixth generation, the death rate fell from the horrific baseline of 67 percent to a mere 8 percent. Total eggs produced per hen jumped from 91 to 237, mostly because the hens started living longer, but also because they laid more eggs per day. The group-selected hens were more productive than were those subjected to individual-level selection. They also actually looked like the pictures of chickens you see in children’s books—plump and well-feathered, in contrast to the battered, beaten-up, and partially defeathered hens that resulted from individual-level selection.

Humans were probably never subjected to such a strong and consistent selection pressure as were those foxes and hens, so it would take more than six or ten generations to produce novel traits in humans. But how much longer? Can the human genome respond to new selection pressures in, say, 30 generations (600 years)? Or would it take more than 500 generations (10,000 years) for a new selection pressure to produce any genetic adaptation?

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[^1]: Muir 1996.
The actual speed of genetic evolution is a question that can be answered with data, and thanks to the Human Genome Project, we now have that data. Several teams have sequenced the genomes of thousands of people from every continent. Genes mutate and drift through populations, but it is possible to distinguish such random drift from cases in which genes are being “pulled” by natural selection. The results are astonishing, and they are exactly the opposite of Gould’s claim: genetic evolution greatly accelerated during the last 50,000 years. The rate at which genes changed in response to selection pressures began rising around 40,000 years ago, and the curve got steeper and steeper after 20,000 years ago. Genetic change reached a crescendo during the Holocene era, in Africa as well as in Eurasia.

It makes perfect sense. In the last ten years, geneticists have discovered just how active genes are. Genes are constantly turning on and off in response to conditions such as stress, starvation, or sickness. Now imagine these dynamic genes building vehicles (people) who are hell-bent on exposing themselves to new climates, predators, parasites, food options, social structures, and forms of warfare. Imagine population densities skyrocketing during the Holocene, so that there are more people putting more genetic mutations into play. If genes and cultural adaptations coevolve in a “swirling waltz” (as Richerson and Boyd put it), and if the cultural partner suddenly starts dancing the jitterbug, the genes are going to pick up the pace too. This is why genetic evolution kicked into overdrive in the Holocene era, pulling along mutations such as the lactose tolerance gene, or a gene that changed the blood of Tibetans so that they could live at high altitudes. Genes for these recent traits and dozens of others have already been identified. If genetic evolution was able to fine-tune our bones, teeth, skin, and metabolism in just a few thousand years as our diets and climates changed, how could genetic evolution not tinker with our brains and behaviors as our social environments underwent the most radical transformation in primate history?

I don’t think evolution can create a new mental module from scratch in just 10,000 years, but I can see no reason that existing features—such as the six foundations I described in chapters 7 and 8, or the tendency to feel shame—would not be tweaked if conditions changed and then stayed stable for a thousand years. For example, when a society becomes more hierarchical or entrepreneurial, or when a group takes up rice farming, herding, or trade, these changes alter human relationships in many ways, and reward very different sets of virtues. Cultural change would happen very rapidly—the moral matrix constructed upon the six foundations can change radically within a few generations. But if that new moral matrix then stays somewhat steady for a

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82 See Hawks et al. 2007; Williamson et al. 2007. The short explanation is that you examine the degree to which each gene tends to pull neighboring DNA along with it as it goes through the chromosomal shuffle of meiosis. If it’s just random drift, then neighboring nucleotides don’t get dragged along.

83 Richerson and Boyd 2005 note that when environments change rapidly, such as every few millennia, the genes don’t respond; all adaptation is done by cultural innovation. But they formulated their theory back when everyone thought genetic evolution required tens or hundreds of thousands of years. Now that we know that genes can respond within a single millennium, I think my statement here is accurate.

84 Yi et al. 2010.


86 See e.g., Clark 2007.
few dozen generations, new selection pressures will apply and there could be some additional gene-culture coevolution.\textsuperscript{87}

Fast evolution is Exhibit D in the retrial of group selection. If genetic evolution can be fast, and if the human genome coevolves with cultural innovations, then it becomes quite possible that human nature was altered in just a few thousand years, somewhere in Africa, by group selection during particularly harsh periods.

For example, the climate in Africa fluctuated wildly between 70,000 and 140,000 years ago.\textsuperscript{88} With each swing from warmer to cooler, or from wetter to drier, food sources changed and widespread starvation was probably common. A catastrophic volcanic eruption 74,000 years ago from the Toba volcano in Indonesia may have dramatically changed the Earth’s climate within a single year.\textsuperscript{89} Whatever the cause, we know that almost all humans were killed off at some point during this time period. Every person alive today is descended from just a few thousand people who made it through one or more population bottlenecks.\textsuperscript{90}

What was their secret? We’ll probably never know, but let’s imagine that 95 percent of the food on Earth magically disappears tonight, guaranteeing that almost all of us will starve to death within two months. Law and order collapse. Chaos and mayhem ensue. Who among us will still be alive a year from now? Will it be the biggest, strongest, and most violent individuals in each town? Or will it be the people who manage to work together in groups to monopolize, hide, and share the remaining food supplies among themselves?

Now imagine starvations like that occurring every few centuries, and think about what a few such events would do to the human gene pool. Even if group selection was confined to just a few thousand years, or to the longer period between 70,000 and 140,000 years ago, it could have

\textsuperscript{87} Some readers may fear, as perhaps Gould did, that if genetic evolution continued during the last 50,000 years, then there could be genetic differences among the races. I think such concerns are often overstated. There were few selection pressures that ever applied to all Europeans, or all Africans, or all Asians. Continent-wide races are not the relevant units of analysis for the evolution of morality. Rather, there were many selection pressures facing each group that moved into a new ecological niche, or that took up a new way of making a living, or that developed a particular way of regulating marriages. Furthermore, when gene-culture coevolution favored certain traits, these traits were usually adaptations to some challenge or other, so differences among groups do not imply defects. And finally, even if there do turn out to be ethnic differences in moral behavior that are related to genetic differences, the genetic contribution to such behavioral differences would likely be tiny compared to the effects of culture. Anyone could have made up a just-so story in 1945 to explain how Germans evolved to be so well suited to militaristic conquest while Ashkenazi Jews evolved to be meek and pacificist. But fifty years later, comparing Israel to Germany, they’d have to explain the opposite behavioral pattern. (I thank Steven Pinker for this example.)

\textsuperscript{88} Potts and Sloan 2010. See also Richerson and Boyd 2005 for a theory about how an earlier period of climatic instability may have driven the first jump in humanity’s transformation into cultural creatures, around 500,000 years ago.

\textsuperscript{89} Ambrose 1998. Whether or not this specific volcanic eruption changed the course of human evolution, I’m trying to make the larger point that evolution is not a smooth and gradual process, as is assumed in most computer simulations. There were probably many “black swan” events, the highly improbable events described by Taleb (2007) that disrupt our efforts to model processes with just a few variables and some assumptions based on “normal” conditions.

\textsuperscript{90} Potts and Sloan 2010.
given us the group-related adaptations that allowed us to burst forth from Africa soon after the bottleneck to conquer and populate the globe.\textsuperscript{91}

\textit{It’s Not All About War}

I’ve presented group selection so far in its simplest possible form: groups compete with each other as if they were individual organisms, and the most cohesive groups wipe out and replace the less cohesive ones during intertribal warfare. That’s the way that Darwin first imagined it. But when the evolutionary psychologist Lesley Newson read an early draft of this chapter, she sent me this note:

I think it is important not to give readers the impression that groups competing necessarily meant groups being at war or fighting with one another. They were competing to be the most efficient at turning resources into offspring. Don’t forget that women and children were also very important members of these groups.

Of course she’s right. Group selection does not require war or violence. Whatever traits make a group more efficient at procuring food and turning it into children makes that group more fit than its neighbors. Group selection pulls for cooperation, for the ability to suppress antisocial behavior and to spur individuals to act in ways that benefit their groups. Group-serving behaviors sometimes impose a terrible cost on outsiders (as in warfare). But in general, groupishness is focused on improving the welfare of the ingroup, not on harming an outgroup.

\textit{In Sum}

Darwin believed that morality was an adaptation that evolved by natural selection operating at the individual level \textit{and} at the group level. Tribes with more virtuous members replaced tribes with more selfish members. But Darwin’s idea was banished from the academic world when Williams and Dawkins argued that the free rider problem dooms group selection. The sciences then entered a three decade period during which competition \textit{between} groups was downplayed and everyone focused on competition among individuals \textit{within} groups. Seemingly altruistic acts had to be explained as covert forms of selfishness.

But in recent years new scholarship has emerged that elevates the role of groups in evolutionary thinking. Natural selection works at multiple levels simultaneously, sometimes including groups of organisms. I can’t say for sure that human nature was shaped by group selection—there are scientists whose views I respect on both sides of the debate. But as a

\textsuperscript{91}The latter part of this period is when the archaeological record begins to show clear signs of decorated objects, beads, symbolic and quasi-religious activities, and tribal behavior more generally. See Henshilwood et al. 2004 on findings from Blombos Cave in South Africa, circa 75,000 years ago. See also Kelly 1995; Tomasello et al., Forthcoming; Wade 2009. Something interesting was going on in Africa between 70,000 and 80,000 years ago.
psychologist studying morality, I can say that multilevel selection would go a long way toward explaining why people are simultaneously so selfish and so groupish.  

There is a great deal of new scholarship since the 1970s that compels us to think anew about group selection (as a part of multilevel selection). I organized that scholarship into four “exhibits” that collectively amount to a defense of group selection.

Exhibit A: major transitions produce superorganisms. The history of life on Earth shows repeated examples of “major transitions.” When the free rider problem is muted at one level of the biological hierarchy, larger and more powerful vehicles (superorganisms) arise at the next level up in the hierarchy, with new properties such as a division of labor, cooperation, and altruism within the group.

Exhibit B: Shared intentionality generates moral matrices. The Rubicon crossing that let our ancestors function so well in their groups was the emergence of the uniquely human ability to share intentions and other mental representations. This ability enabled early humans to collaborate, divide labor, and develop shared norms for judging each other’s behavior. These shared norms were the beginning of the moral matrices that govern our social lives today.

Exhibit C: Genes and cultures coevolve. Once our ancestors crossed the Rubicon and began to share intentions, our evolution became a two-stranded affair. People created new customs, norms, and institutions that altered the degree to which many groupish traits were adaptive. In particular, gene-culture coevolution gave us a set of tribal instincts: we love to mark group membership, and then we cooperate preferentially with members of our group.

Exhibit D: Evolution can be fast. Human evolution did not stop or slow down 50,000 years ago. It sped up. Gene-culture coevolution reached a fever-pitch during the last 12,000 years. We can’t just examine modern-day hunter-gatherers and assume that they represent universal human nature as it was locked into place 50,000 years ago. Periods of massive environmental change (as occurred between 70,000 and 140,000 years ago) and cultural change (as occurred during the Holocene era) should figure more prominently in our attempts to understand who we are, and how we got our righteous minds.

92 For an attempt to explain human groupishness without invoking group selection, see Tooby and Cosmides 2010. See also Henrich and Henrich 2007; they allow for cultural group selection, but with no genetic effects. I think these approaches can explain much of our groupishness, but I don’t think they can explain things like the hive switch, which I describe in the next chapter.

93 These issues are all complicated, and as a social psychologist I am not an expert in any of the four areas I have reviewed. So it may be more accurate to describe my presentation not as a defense in a legal trial, but as an appellate brief to the high court of science explaining why I think the case should be re-opened and re-tried by the experts, in light of the new evidence.
Most of human nature was shaped by natural selection operating at the level of the individual. Most, but not all. We have a few group-related adaptations too, as many Americans discovered in the days after 9/11. We humans have a dual nature—we are selfish primates who long to be a part of something larger and nobler than ourselves. We are 90 percent chimp and 10 percent bee. If you take that claim metaphorically, then the groupish and hivish things that people do will make a lot more sense. It’s almost as though there’s a switch in our heads that activates our hivish potential when conditions are just right.

94 The numbers 90 percent and 10 percent should not be taken literally. I am just trying to say that most of human nature was forged by the same sorts of individual-level processes that forged chimpanzee nature, while a substantially smaller portion of human nature was forged by group-level selection, which is a process more commonly associated with bees, ants, and other eusocial creatures. Of course the psychology of bees has nothing in common with human psychology—they achieve their extraordinary cooperation without anything like morality or the moral emotions. I’m merely using bees as an illustration of how group-level selection creates team players.