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THE EVOLUTION OF COOPERATION

Halfway through high school I discovered *Cracked* comics, edgier than the better-known *Mad.* I painstakingly copied onto my school briefcase, in light green house paint, an image I found there: Albert the Alligator from *Pogo* (as I retrospectively realize) with a two-yard-long screw skewering his midriff, framed in the caption: "Do Unto Others . . . Then Cut Out." Forty years on I can't resurrect the impulse that made this image so irresistible. I can only suppose that a standing alligator blithely sporting a gigantic screw tickled my fancy, and that at fifteen and chafing at adult proprieties I liked even more the parodic affront to the Golden Rule, "Do unto others as you would have them do unto you," the implicit "Screw you," in slang new to me. I must have copied out image and text in what I thought a protest against conformity. But not for a moment did I call into question the Golden Rule itself. Precisely because it made such universal good sense, pretending to subvert it seemed to my teenage self a perfect provocation.

Why does the Golden Rule make such sense to us all? Why do we cooperate, even when we might also itch to rebel?

Cooperation has been a prime focus of sociobiology and its offshoot evolutionary psychology. In the mid-1960s William Hamilton and George Williams transformed evolutionary theory by turning sociality from an accepted fact into a scientific problem.[1] Darwin, always aware of difficulties his theory needed to confront, had been troubled by eusociality in ants and bees, in whose colonies most renounce their reproductive rights. But before Hamilton and Williams, others less inclined to confront difficulties had been able to think that individuals could easily evolve to act for the good of their group or species, a position now known as "naïve group selectionism." Hamilton and Williams made clear how hard it was to explain the cooperation necessary for social life. If one animal behaves for the good of others—draws attention to predators or fights them off, for instance, at risk to itself, or forgoes a share of food because others are hungry—but another does not, the second will be more likely to survive. Its more selfish genes will be more likely to pass to the next generation than the genes of the more selfless. Over time, cooperative genes should therefore die out and uncooperative genes come to dominate in any population.

Biology rules out invariably unstinting altruism. Any creature that never, regardless of context, behaved first for itself could be easily exploited by others. It would be unlikely to last long enough to reach the age of reproduction, and if it lasted that far, it would get no further. The ultimate unconditional altruist would be a male who refrained from sex in favor of other males, to help *their* genes, rather than his own, into the next generation.[2] He could have no heirs. Yet if unconditional altruism is impossible, conditional cooperation exists. But how could it establish itself?

The challenge to explain rather than merely to accept sociality, and to do so in terms of strict genetic accounting, led to the new disciplines of sociobiology in the 1970s and, in the 1980s, evolutionary psychology, which has particularly probed the psychological mechanisms enabling sociality. ~~Much of the energy of early sociobiology drove research programs (Hamilton's inclusive fitness theory, Dawkins' selfish gene theory, John Maynard Smith's evolutionary game theory) proposed as alternatives to group selectionism. Recently however these programs and their leading proponents have come to accept the need for *multilevel selection theory,* which rests on one key postulate: "*Selfishness beats altruism within single groups. Altruistic groups beat selfish groups.*"~~[3] ~~Other things being equal, selfishness—reaping a benefit without contributing a full share of the cost—pays most in the short term. But in the long term cooperation can often yield more, enabling a group to achieve more than the sum of what its members could achieve individually, whether that be building hives or dams, for bees or beavers, or hunt-~~

~~ing large prey, for hyenas or humans, and thereby to outcompete other groups.~~

~~Multilevel selection theory retains the competitiveness that drives natural selection, and like early sociobiology rejects naïve "for-the-good-of-the-group" thinking.~~[4] ~~It explains how cooperation, like other traits impossible to establish at a given level, can in principle establish itself, can earn its competitive keep, by offering advantages in competition between higher-level units. *In principle:* but it also requires that any adaptive trait be assessed on a case-by-case basis, to see which levels of selection have been most powerful in shaping that particular trait: the individual or some higher-level group.~~

~~Multilevel selection theory also makes it more possible to see the history of life as a series of major transitions in which cooperation has been established (or competition suppressed) at one level, enabling greater cooperation and complexity at another level: the coordination of complex molecules to produce the first self-replicating organisms, the first life; the symbiosis of two bacterial cells, without nuclei, into the eukaryotic or nucleated cell; the integration of cells into multicellular organisms; the cooperation of individuals in social groups; and the special cases of eusociality—ant colonies, beehives, termite mounds, and the like, which function in effect as superorganisms—and human ultrasociality.~~[5] ~~Human cooperation enables millions of individuals and myriad groups with distinct purposes to cooperate on a more-than-local and sometimes a global scale.~~

~~Our increased cooperativeness, many researchers now believe, may also be the key to the runaway growth of human intelligence. Through greater motivation to share emotions, attention, intentions, and information, we have learned to understand other perspectives and to detach thought from the immediate; we have developed language and what we could call human ultraculture.~~[6] ~~Culture easily amplifies group differences, and hence the force of group selection, since although genetic mutations can spread only over generations, cultural changes with significant effects on the relative fitness of groups can spread within a single generation.~~[7]

But how could cooperation begin, if evolution operates on only immediate rather than future advantages, and if in the short term selfishness offers greater rewards than cooperation does? Cooperation poses a difficult engineering problem,[8] but since its advantages can be so substantial, and since nature has had so much time for trial and error, natural selection has found a suite of partial but surprisingly effective solutions.[9]

Biologists call the first solution *mutualism:* individuals help one another merely as each pursues its own interests.[10] If I watch for predators as I forage for food, I can benefit from the vigilance, and be alerted by the alarm, of my neighbors if they are close enough to face the same threat. In prey species natural selection gradually favored those most inclined to stay together. To restate in design terms: evolution engineered a first step to sociality by inculcating in animals with few natural defenses a sense of comfort in the presence of conspecifics and of unease at straying far from them. An isolated monkey will repeatedly pull a lever with no other reward than to glimpse another.[11] We, too, are "intrinsically a group-living ape" and dread the thought of being excluded from our group.[12]

The sense of empathy with others of one's kind, the positive feeling of shared purposes, underlies all sociality, but it can readily be overridden by the need to compete for resources like space and food that become scarcer with group living. How, then, can sociality develop still further?

The next step, *active* cooperation, could come as natural selection favored those whose behavior helped promote their genes not only in themselves but in others. In the most obvious case, parents predisposed to care for their offspring improve the chances that their own genes will survive and reproduce. Their offspring will inherit a high proportion of their genes, and therefore also their predisposition to promote *their* survival and reproduction. That genes for parental care should be powerfully selected for seems a no-brainer to us precisely because evolution has designed parental care so well that we take it for granted.

Hamilton generalized the principle at work here as *inclusive fitness* (or *kin selection*), a sort of selfishness slightly beyond the self, not only for ourselves but also for copies of our genes in others. This, the "central theorem of selfish gene theory," has been confirmed in hundreds of species.[13] If the cost to me of producing a benefit to a relative is less than the benefit to the other divided by its relation to me (if $C_a < B_b/r$), then evolution should favor my offering the benefit, since it will have a net beneficial effect on *my* genes, albeit within the bodies of others.

~~By now caring for kin seems not quite such a no-brainer. It does not mean however that I have to calculate the formula, whether I happen to be a tree shrew or a human hunter-gatherer; rather it means that natural selection has run the calculation over many generations and built it into my emotions: we "execute evolutionary logic not via conscious calculation, but by following [our] feelings, which were designed as logic executers."~~[14] ~~Natural selection, by favoring us if we favor our close kin, thereby also selects for the genes that *incline* us to such helping behavior, via, for instance, neurotransmitters like oxytocin, which in mammals fosters social recognition and bonding. On average we have been designed by evolution to feel strongly attached to our parents, offspring, and siblings (to each of whom we are related by, on average, 50 percent of our variable genes),~~[15] ~~less strongly attached to grandparents or grandchildren (25 percent), and still less to aunts, uncles, nephews, nieces (12.5 percent), and should on average feel inclined to help each according to the coefficient of relatedness.~~

~~The theory of *parental investment* among other things explains family *conflict* as well as cooperation in terms of genetic relatedness.~~[16] ~~Parental investment includes any expenditure of resources on one offspring that would take from the resources (time, energy, food, and so on) needed to rear others. Parents can produce many children, and it will be in their interest to do so unless intense investment in fewer children would produce better results in terms of survival and eventual reproduction, as in mammalian rather than reptilian reproductive systems.~~

~~In diploid species such as mammals, parents are genetically related by 50 percent to each of their children, but each child is related 100 percent to itself and only 50 percent to its actual or potential siblings. Each child should therefore prefer parents to invest in *it*, unless the same investment would benefit at least two other actual or potential siblings by at least the same amount or benefit one other by at least twice as much. Each offspring should therefore prefer to concentrate~~

~~its parents' investment in itself—in mammals, for instance, through continued breast-feeding—while its parents should prefer to maximize their genetic transmission to the next generation by offering, on average, equal investment in each of their present and future offspring. Here we see why even in the most cooperative of relationships competition is inevitable, and why the powerful emotions engendered by family loyalty and conflict saturate stories from Genesis to *The Sopranos*.~~

If cooperation is fairly easy to establish, yet already fraught, among close kin, how can it extend even among non-kin? Game theory studies interactions in which one party's success depends to some extent on moves made by others with competing interests. In a zero-sum game like chess or tennis, your gain is my loss. In a non-zero-sum game, both of us can gain or lose different amounts. The prisoner's dilemma is the classic non-zero-sum model of the complications of cooperation.[17]

Imagine, Peter Singer asks, that you and another prisoner are sitting in separate cells of a Ruritanian prison, charged with plotting against the state. There is too little evidence to convict either of you. If you confess and the other prisoner does not, he will get twenty years and you will go free, and vice versa. If both of you confess, each of you will get ten years. If neither confesses, both of you will be held for six months under emergency regulations.

> The prisoner's dilemma is whether to confess or not. Assuming that the prisoner wishes to spend the minimum time in prison, it would seem rational to confess. No matter what the other prisoner does, that will be to the advantage of the confessing prisoner. But each prisoner faces the same dilemma, and if they are both to follow their own individual interests and confess, they will end up serving ten years, when they could have been out in six months!
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> There is no solution to this dilemma. It shows that the outcome of rational, self-interested choices by two or more individuals can make all of them worse off than they would have been had they not pursued their own short-term self-interest.[18]

If each cooperates with the other, if each *trusts* the other enough, both can save years in prison, but if either assumes that the other can be trusted, but is wrong (the other "defects"), he or she gets the sucker's payoff, twenty years. Cooperation may be best, but how can the trust on which it depends be established securely enough to make the risks worthwhile? Singer offers an everyday modern example. If we all took buses to work, the roads would be unclogged, and we would get there faster. But since we do not trust that enough others will opt for buses, we continue to drive our cars, since if the roads remain clogged, cars will at least be faster than buses.

To explain how cooperation in non-kin evolves, we need to combine Hamilton's gene-centered view of evolution with game theory to generate *reciprocal altruism:* I help you in the expectation that you may help me later.[19] Such cooperation can extend far beyond relatives, and therefore bring many more of the benefits of cooperation, but like the prisoner's dilemma, it faces the risks of defection by the party that owes the return favor.

In a single prisoner's-dilemma situation, it always pays to defect. But in indefinitely repeated encounters, players may see that both will lose unless they trust each other. If you and I live in close proximity and are likely to encounter each other repeatedly, we have reason to develop the trust that can earn us the benefits of active cooperation. Reciprocal altruism can most readily begin, therefore, among individuals living in small, settled groups—where many may also be related.[20]

Even so, there still lurks the danger of defection, of failing to repay. Cheaters will thrive in exchanges with altruists unless altruists discriminate against—refuse further exchange with, or actively punish—cheaters. If they discriminate against cheaters, altruists will exchange only with other altruists and benefit from their cooperation, while cheaters will be left to deal with other cheaters and reap no net benefit. On this condition altruists can outcompete cheaters and, in evolutionary terms, ultimately outreproduce them.

For altruism to work robustly a whole suite of motivations has to be in place: sympathy, so that I am inclined to help another; trust, so that I can offer help now and expect it will be somehow repaid later; gratitude, to incline me, when I have been helped, to return the favor; shame, to prompt me to repay when I still owe a debt; a sense of fairness, so that I can intuitively gauge an adequate share or repayment; indignation, to spur me to break off cooperation with or even inflict punishment on a cheat; and guilt, a displeasure at myself and fear of exposure and reprisal to deter me from seeking the short-term advantages of cheating. We can reverse-engineer the social and moral emotions so central to our engagement with others in life and in story.[21] Rather than merely taking these emotions as givens, we can account for them as natural selection's way of motivating widespread cooperation in highly social species.[22]

Reciprocal altruism among non-kin has since been documented in vampire bats, which share surplus blood with other sharers but withhold from nonsharers,[23] and has been tested experimentally among primates. Capuchin monkeys will share more with partners who have helped them with food or grooming.[24] Baboons offer social support.[25] Chimpanzees and bonobos tally services they have received, return favors (food, sex, grooming, support, or nonintervention in power struggles), and can even show indignation when an ally who owes them support fails to deliver.[26]

Apart from theory, observation, and behavioral experiments, those studying the evolution of cooperation have found another way to clarify how cooperation could emerge. Computer simulations using weighted costs and benefits in iterated prisoner's-dilemma encounters make it possible to test multiple strategies against one another, over hundreds or thousands of cycles, to see which fares best in competition against whatever other strategies, nice or nasty, simple or complex, programmers can devise.

Academics from around the world have devised computer-programmed strategies to test the constraints on cooperation and pitted them against one another in computer tournaments.[27] Surprisingly, the simplest strategy, Tit for Tat, won the first such tournament: cooperate on the first move, then copy your partner's last move. If the partner cooperates, cooperate; if it defects, defect. In a second tournament even strategies designed specifically to counter Tit for Tat's success could not do so, although variations on this basic design (like Contrite Tit for Tat, Generous Tit for Tat, Suspicious Tit for Tat) have since been shown to fare even better under some conditions:

> as we carefully develop these models, adding complications one by one, a profile of traits emerges that many would regard as uniquely human—niceness, retaliation, forgiveness, contrition, generosity, commitment . . . and self-destructive revenge. It is amazing that such a human profile of traits emerges so naturally from such simple models based entirely on the survival of the fittest.
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> . . . The capacity to forgive should extend far beyond us and our primate ancestors to any creature with sufficient brainpower to employ TFT-like rules. Even guppies have been shown to qualify . . . They recognize their social partners as individuals, behave according to their own dispositions at the start of relationships, and become less altruistic in response to selfish partners. They try to associate with altruistic partners regardless of their own degree of altruism.[28]

Building on the work of Hamilton and others, psychologist Leda Cosmides realized that if humans are to benefit from social exchange, we must always be alert for cheating. She saw that this requirement might offer a test of how our minds work. Do we assess information in a content-independent, general-purpose way, or do we assess it, when facing problems recurrent throughout our past, in ways shaped by evolution to deal with these particular situations?

Cosmides showed that a common test of purely logical reasoning, the Wason Selection Task, normally difficult for most to solve, turns out to be very easy to pass when it takes the form of a problem involving cheating in social exchange.[29] In the Wason test we are asked which of four cards we must turn over to test whether a proposition is valid. For instance, if the proposition is "If a person is a Leo, then that person is brave" and there are four cards with an astrological sign on one side and a rating of courage on the other, the face-up sides being "Leo," "brave," "Aries," and "coward," then most of us realize we have to turn over the "Leo" card, many think we also have to turn over the "brave" card, and considerably fewer realize that in fact we need to turn over both the "Leo" and the "coward" cards and no more. If we had special circuits for logical reasoning, we would see that *If P then Q* needs to be tested against both *P* and *not-Q,* but usually "fewer than 10% of subjects spontaneously realize this."[30]

When the content of the question changes so that it requires us to look for cheaters in social exchange, the performance jumps dramatically, to 70–90 percent, the highest ever recorded for the test, even when the situation described is culturally unfamiliar and deliberately bizarre (for instance: "If a man eats cassava root, then he must have a tattoo on his face"). Success remains high even with these unfamiliar scenarios, but only if they are set up as social contracts, not if they are presented as noncontractual situations based on the same bizarre condition. Cosmides then "tested unfamiliar social contracts that were *switched*" so that the correct social-contractual result was now the wrong logical response. Seventy-one percent still answered with "the 'look for cheaters' response, *not-P and Q,* . . . even though this response is illogical according to the propositional calculus."[31]

People who cannot usually detect violations of "if-then" rules can do so easily when the violation involves cheating in social exchange.[32] No one had thought, until evolutionary theory showed the constraints on evolving social exchange, to expect minds prepared to identify cheating, and colleagues thought Cosmides crazy even to investigate.[33]

~~Cosmides and her husband and coworker John Tooby ascribe the results to a cheater-detection module. I would prefer to call it a subroutine and to define its role as emotional highlighting rather than detection. We are indeed wary of cheating, and discrepancies between voice tone and facial expression or posture may place us on guard, but we have no sure way of *detecting* concealed cheating. Evolution has not made us Sherlock Holmeses, but when we *recognize* behavior that crosses a social rule, it springs out to our attention.~~

That quibble aside, Cosmides' findings are so striking that they have been repeatedly challenged and tested by those inside and outside evolutionary psychology. The debate still continues, as it does at the forefront of any science, but in every case so far Cosmides and Tooby and their colleagues have rerun or extended the tests, from logic students to hunter-gatherers, and have shown that proposed alternative explanations cannot account for their results.[34] Neuroimaging experiments also show activation in brain areas used for reasoning about social exchange rather than in areas used for reasoning about logically similar behavioral rules.[35] It really does seem that even on what might appear to be higher-level and domain-general problems, even on the logic of the Wason test, even in highly conscious mental problem-solving, our thoughts can be strongly guided by evolved predispositions.

~~Not only three-year-old humans, but even animals with tiny brains, like guppies or cleaner fish, seem to be able to solve such problems—obviously not via Wason tests, but as observed by biologists. This predisposition seems an element of social behavior that stretches far back into social exchange between unrelated individuals, and for that reason this highly focused system works more efficiently than our general-purpose logical reasoning: the answers pop out to our attention~~.

Across human cultures and in many other species individuals incline to punish others for cheating. In our case at least, our emotions not only alert us to register unfairness but also motivate us to punish it, because in the long run doing so improves the chances of our benefiting from cooperation.

Recent work in evolutionary economics has shown that in other respects, too, we, like other species, work less by reason, the economists' assumption of "rational individuals," than through emotions primed by evolution. In neoclassical economics, individuals are assumed to behave "rationally," to seek to maximize their gains. This assumption would predict that if we are offered real money for nothing, we will not turn it down. But in experiments people repeatedly reject profit in order to satisfy their sense of justice.[36]

In one experiment, the dictator game, two strangers play for (usually real) money, say $100. I, as dictator, must offer you a share. If you accept the division, both of us keep our agreed portions. If you reject the offer, neither of us receives anything. In terms of strict economic rationality, an offer of a dollar, even a cent, would leave the second participant better off, and should therefore be accepted. But even as you read this, I expect you recoil at the thought of such measly offers. Participants in the experiment behave the same way. No dictator proposes such token sums but tends to offer amounts closer to $50. Often if the sum offered is only a little under $40, the respondent rejects it. A sense of fairness in social exchange overrides the rational calculation of gain. We have evolved not to be "rational individuals," profit maximizers, but social animals, holding others to fair dealings even at our own cost.

Culture inflects the results of these experiments. In fifteen different societies, the average amount the dictators offered varied between 15 percent (in a low-trust society) and 58 percent (in a society sustained by the intense cooperation necessary for dangerous communal deep-sea fishing), but in ten out of fifteen societies the average was 50 percent. Local ecological and cultural conditions can modify the parameters, yet everywhere we act on a sense of fairness rather than on a "rational" pursuit of pure profit.[37]

The same sort of "irrationality" exists for the same reasons in creatures with much smaller brains than ours. Capuchin monkeys are known to be good cooperators. Experimenters gave each monkey a token, then, with hand outstretched, palm up, solicited the token in return for a slice of cucumber. The monkeys happily exchanged a token each time for cucumber, although it is not their favorite food. But then unfairness was introduced. In sight of one monkey, another was given for its token not a slice of cucumber but a much more appealing juicy big grape. When the other was then offered a slice of cucumber for *its* token, it reacted angrily in 40 percent of trials. When one monkey received a grape without even needing to pay a token, the other, four times out of five, refused to hand over its token or to take the proffered cucumber unless to toss it away in disgust.[38]

Humans have far more complex cooperative relationships than capuchins or chimpanzees. We cooperate enough to live in cities of millions. How have we managed to extend cooperation not only beyond nonrelatives but even to complete strangers? How is this possible, especially, when the best conditions for the emergence of reciprocal altruism are indefinitely repeated encounters between individuals settled close to one another?

Of course human cooperation does often break down. Crime simmers or seethes in all large cities. Nevertheless we have achieved remarkable results through building on our evolved dispositions, both our positive and our punitive feelings, our desire to punish cheats. But free-riding, taking benefits without paying the full cost, persists as the fundamental problem of social life.[39] Yet a real if imperfect solution has come through social control—in terms of multilevel selection theory, suppressing within-group selection—rather than through highly self-sacrificial altruism: through second-order punishment, discriminating against and punishing not only cheaters but also those who fail to discriminate against or punish them.[40]

Detecting and punishing others incurs real and substantial costs, as taxpayers paying for police or prisons know. This was the case even before there were detectives and detention centers. Discovering a transgression when someone aims to hide it or confronting someone who has cheated can be costly in time, energy, and risk. Just as we face a first-order temptation to take the benefits of cooperation without the costs, so we can face a second-order temptation to hang back, to reap the benefits of the cooperativeness that others maintain by enforcing the detection and punishment of cheaters. But if I fail to notice or punish cheaters but am noticed and punished for my failure, the advantages of my second-order free-riding rapidly diminish. Soon few will avoid playing their part in detecting and punishing cheaters. Second-order punishment in turn rapidly discourages first-order cheating and makes the second-order cost of monitoring it relatively light, since everybody contributes. So long as people share similar notions of what constitutes cheating, the need for vigilance, and ways it should be dealt with, few will dare step out of line. The social monitoring already intense elsewhere in the primate line becomes still more intense for humans—and a powerful prompt for storytelling.[41]

To extend cooperation through still larger and looser populations, however, we need additional measures, especially cultural ones like shared norms and institutions. You and I need not only to share norms but also to *know* we share them, so that we feel the pressure not only to resist the temptation to cheat but also to resist the temptation not to slacken in dealing with others who cheat.

In small-scale societies, uncooperative acts were often punished through personal revenge, motivated by an evolved sense of outrage but often leading to destructive cycles of vengeance. Especially in larger societies, better means were needed. Centralized systems of justice, and eventually a police force, could detect transgressions, assess charges, and administer punishment. Depersonalizing justice could dampen incendiary emotions and diminish vendettas.

But even before such cultural systems were invented, other ways of motivating cooperation emerged. One was through story. Stories arose, as we will see, out of our intense interest in social monitoring. They succeed by riveting our attention to social information, whether in the form of gossip—indirect but real and relevant social information—or fiction—admittedly invented and heightened versions of the behaviors we naturally monitor. Modern hunter-gatherer societies preserve their strong egalitarianism by gossip, sharing reports of anyone seeking status, and by admonitory stories warning against violating egalitarian norms.[42] And in societies of any size, stories involving agents with unusual powers capture attention and commandeer memory, and stories with unseen agents who can monitor our behavior and administer punishment or reward—the stories we call religion—permeate and persist partly because they offer such powerful ways of motivating and apparently monitoring cooperative behavior. Religious stories establish a secret spirit police.[43]

In both factual and fictional forms, stories can consolidate and communicate norms, providing us with memorable and shared models of cooperation that stir our social emotions, our desire to associate with altruists (like Dr. Seuss's Horton), and our desire to dissociate ourselves from cheats and freeloaders (like the suitors whom the *Odyssey* repudiates and Odysseus routs). Such memorable images of pro- and antisocial characters and actions common to whole communities can not only define and communicate shared standards but ensure that all know what others know of these standards.[44] As we will see, stories have multiple origins and functions, but among them not least is that they have so often discouraged defection and aided cooperation. *Graphing Jane Austen*, a recent internet study of readers' responses to the characters of nineteenth-century British novels, confirms our folk sense of the polarizing power of the goodie-baddie axis and its centrality in our responses to fiction.[45]

Our continually refined methods of prevention, detection, conviction, and punishment allow us to coexist in societies of many millions. Let us hope we will continue to find even better solutions. But we could not have started on this path without evolved dispositions for cooperation or have advanced as far as we have without elaborating them through culture.

Research of the last few decades in evolutionary theory and game theory, in biological field study and experiment, and in evolutionary psychology and economics shows how cooperation can evolve in creatures with different genes and, to that extent, different interests. It emerges from shared needs, in *mutualism;* from shared genes, in *inclusive fitness;* from shared impulses, in *empathy;* from common interests over time, in *reciprocal altruism;* and from a shared recognition of the benefits of cooperation, even on a large scale, incorporated by nature into our *emotions,* our sense of fairness, our wariness against cheating, our indignation and readiness to punish cheaters, and incorporated by culture into our *norms, institutions,* and *narratives.*

Some who look at human nature through evolutionary lenses argue that our intelligence allows us to overcome—to say no to—our genes. It does: we can inhibit ourselves through conscious reflection, through cultural norms, through the fear of social sanctions. Others argue that our genes themselves give rise to the suite of moral emotions that we partly share with other social animals and motivate us to *want* to inhibit our more selfish impulses.[46] They, too, are right. Although our genes compete with one another, many of our evolved emotions also point us toward cooperation, because its benefits are so substantial, and we can use our intelligence and our sociality—also aspects of our evolved nature—to devise still better solutions to the problems of cooperation.

Evolution offers a much more complex and nuanced view of the social world than the artificial model of the rational individual of economics, or the romantic idea, common since Rousseau, of good people perverted by evil systems, or the paranoid Nietzschean or Foucauldian suspicion that all moral claims mask a lust for power. An evolutionary view of cooperation allows us to look at the social world without inordinate hopes, but with real confidence that we can continue to find better solutions, even to the new problems that the very successes of our cooperation create.

10. ~~Geary 2005: 10. As Geary notes, he refines here the model proposed by Rochel Gelman.~~
11. ~~Geary 2005: 132.~~
12. ~~Humphrey 1976; Alexander 1989; Dunbar 1998a; de Waal and Tyack 2003.~~
13. ~~Alexander 1989; Geary 2005: 60–66; Flinn, Geary, and Ward 2005.~~
14. ~~Geary 2005: 105.~~
15. ~~Geary 2005: 230–233.~~
16. ~~Geary 2005: 232.~~
17. ~~Baddeley and Hitch 1974; Baddeley and Logie 1999; Baddeley 2000.~~
18. ~~Geary 2005: 170.~~
19. ~~Cf. Bonner 1980: 147.~~
20. ~~Geary 2005: 184, 216–217, 272.~~
21. ~~Similar conclusions have been reached by Tooby and Cosmides 2001.~~

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1. W. D. Hamilton 1963, 1964; G. Williams 1966.
2. Radcliffe Richards 2000: 174.
3. D. S. Wilson and E. O. Wilson 2007: 335 and passim.
4. D. S. Wilson and E. O. Wilson 2007: 338.
5. Maynard Smith and Szathmáry 1995; D. S. Wilson and E. O. Wilson 2007: 339–344.
6. Tomasello et al. 2005; D. S. Wilson and E. O. Wilson 2007.
7. Richerson and Boyd 2005; D. S. Wilson 2005.
8. Pinker 1997: 428.
9. See Dugatkin 2002 for an overview.
10. Maynard Smith 1982a: 2 notes that this was often overlooked in early sociobiological accounts of cooperation.
11. Butler 1954; E. O. Wilson 1975/2000: 7.
12. Barash and Barash 2004; Leary and Downs 1995: 128: "human beings appear to possess a fundamental motive to avoid exclusion from important social groups."
13. Hamilton 1963; Dawkins 1989a: 80; Gaulin and McBurney 2001: 320. Nevertheless multilevel selection theory reinterprets Hamilton, as Hamilton himself came to accept: "When Hamilton reformulated his

theory in terms of the Price equation, he realized that altruistic traits are selectively disadvantageous within kin-groups and evolve only because kin-groups with more altruists differentially contribute to the gene pool" (D. S. Wilson and E. O. Wilson 2007: 335).

14. Wright 1996: 190.
15. Reeve 1998: 48: genetic "relatedness is not a measure of the absolute genetic similarity between two individuals, but of the degree to which this similarity exceeds the background similarity between randomly chosen individuals from the population."
16. Trivers 1972, reprinted with discussion in Trivers 2002a: 123–153.
17. See Wright 2000 for the implications of non-zero-sum games in human life.
18. Singer 1999: 47–48.
19. Trivers 1971, reprinted with discussion in Trivers 2002a: 3–55.
20. Trivers 1971; Axelrod and Hamilton 1981; Axelrod 1990.
21. Trivers 1971, 1972, 2002a; Frank 1988; cf. Pinker 1997: 404–405.
22. Pinker 2002: 53.
23. Wilkinson 1984.
24. de Waal 2001a: 366n17.
25. Packer 1977.
26. de Waal 1998: 203.
27. Axelrod 1990.
28. D. S. Wilson 2002: 193.
29. Wason 1966; Cosmides 1989; Cosmides and Tooby 1992.
30. Cosmides and Tooby 1995: 90.
31. Cosmides and Tooby 1989: 91.
32. Cosmides and Tooby 1995: 91.
33. See Cosmides and Tooby 2005 for the most recent discussion.
34. Cosmides and Tooby 2005; Buller 2005; see http://www.psych.ucsb.edu/research/cep/buller.htm.
35. Ermer et al. 2007.
36. Fehr and Henrich 2003.
37. Henrich et al. 2001.
38. Brosnan and de Waal 2003.
39. D. S. Wilson 2002: 8; D. S. Wilson and E. O. Wilson 2007: 336 and passim.

40. See also R. Boyd and Richerson 1992; Fehr and Gächter 2002; D. S. Wilson and E. O. Wilson 2007: 339.
41. Flesch 2007 unwarrantedly makes this almost the sole biological reason for storytelling.
42. Boehm 1993, 2000.
43. D. S. Wilson 2002: 64–65.
44. See Chwe 2001.
45. J. Carroll et al. under submission.
46. No to our genes: Dawkins 1989b; Pinker 1997. Our genes say no: de Waal 1996, 2006.

~~Part 2. Evolution and Art~~

~~*Epigraph:* Cain 1964, quoted in Dawkins 1989a: 31.~~

~~Chapter 5. Art as Adaptation?~~

1. ~~For fuzzy categories, see Rosch 1973 and 1975.~~
2. ~~D. Brown 1991; Dissanayake 1988, 1995, 2000.~~
3. ~~S. Davies 2000: 200, 201.~~
4. ~~Dutton 1993: 21 and 1995: 35.~~
5. ~~Dürer 1971: 24–25, quoted in Dutton 1977: 392; Goethe, conversation with Eckermann, 31 January 1827, quoted in Wright 2000: 155; Japanese: Pinker 2002: 408.~~
6. ~~For animal culture, see Bonner 1980; de Waal 2001a. For the circularity of explaining culture by culture, see de Waal 2001a and Nordlund 2007.~~
7. ~~Dickie 1997: 19.~~
8. ~~Novitz 1996: 162: "We expect that works of art will make us feel more at home in our world."~~
9. ~~Dissanayake 1988: 67, summarizing John Dewey, Herbert Read, and Suzanne Langer.~~
10. ~~Shklovsky 1990.~~
11. ~~For an appreciative survey, from someone interested in both the wide functions of art and an evolutionary perspective on the arts, see Dissanayake 1988: 64–106 and 1995: 10, 84. For brief dismissive catalogues of proposed functions, see G. Miller 1999: 79 and 2000b: 262.~~