

How Can Evolution and Neuroscience Help Us Understand Moral Capacities?

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Trying to understand morality has been a central human preoccupation for as far back as human history extends, and for very good reasons. The core phenomenon is readily observable: we humans judge each other's behaviour as right or wrong, and each other's selves as moral or immoral. If others view you as moral, you will thrive in the bosom of a human group. If, however, others view you as immoral, you are in deep trouble; you may even die young, either at the hands of others, or alone in the bush. These are very good reasons indeed for close attention to morality.

There are, however, two problems. The first is how to distinguish right from wrong, the second is inhibiting temptations to do what is wrong (that temptations to do right are not a problem is most interesting). The first problem poses few concerns for most people – they are confident that they know what is right, based on their intuitive emotional responses. However, different people have different emotional responses, and intuition makes a poor argument. Finding a general principle that explains the individual instances would be incredibly valuable. So, for several thousands of years, philosophers have tried to find general moral principles. They have also argued about where they come from, why they have normative force, and how they are best applied to individual instances (Darwall, Gibbard, & Railton, 1997). Thousands of books chronicle the human quest for moral knowledge.

Now, in a mere eye blink of history, the scene has changed. Completely new kinds of knowledge are being brought to bear. Neuroscience is investigating the brain mechanisms involved in moral decisions, moral actions, and responding to moral and immoral actions by self and others. Evolutionary biology is investigating why those brain mechanisms exist, how they give a selective advantage, and why there is genetic variation that influences moral tendencies. This is an exciting time for those of us curious about morality.

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Before jumping in with new theory and data, however, it is worth stepping back to see how existing explanations fit what we know already. Otherwise, our efforts to help may be received very much like those of a child who holds up his portable video game in a symphony concert and yells excitedly, "Everyone has to try this!" It is impossible to summarize the accomplishments of moral philosophy over even the Western tradition, but three generalizations may be useful. First, general agreement has been reached on some issues. Second, a remarkable amount of disagreement persists. Third, much of the disagreement comes from confusion about what kind of question is at issue, and much of the agreement is about the need to frame questions carefully.

The most fundamental distinction is between descriptive statements and normative statements. One set of questions is descriptive – what are moral capacities and moral behaviors like, and where do they come from? They are about what is. They are, for the most part, science. The other set of questions is normative. They are about what is right and what is wrong. They are about what we ought to do.

The importance of keeping these questions separate is a major recent (as these things go) advance in moral philosophy, attributed usually to David Hume in the 18th century (Hume, 1985 [1740]). Knowing what the world is like cannot directly tell us what is right. Framed in a more familiar form, you cannot get an Ought from an Is. Normative principles about what we should do cannot be derived from knowledge about what the world is like, not even from complete scientific knowledge about the brain and how its moral capacities were shaped by natural selection. (Subtle arguments apply, of course, but those are for another time).

The attempt to derive normative principles from facts is often called the naturalistic fallacy, but that is not exactly accurate. GE Moore, in his 1903 book *Principia Ethica* (Moore, 1903), defined the naturalistic fallacy as attempts to prove a moral claim based on a definition of "good" based on natural properties such as what is desirable or pleasant. Moore's point is that "good" cannot be defined in such terms, because it is not an object in the natural world. This is obviously closely related to the Is-Ought barrier, so, like others, I will use the phrase "naturalistic fallacy" in the more general sense.

While nearly every article on evolution and morals notes the importance of avoiding the naturalistic fallacy, many then go ahead and nonetheless draw moral guidance from observations about the world. Or, if they don't, readers do, often with blissful naïveté. To observe the phenomenon for yourself, explain the naturalistic fallacy to undergraduate students, then explain how natural selection has shaped male mammals to compete to get as many matings as possible, and open the discussion. The fact of increased competition among males leads some students to conclude that such behavior is natural and therefore right. Others will disagree, and the resulting animated exchanges demonstrate how people draw normative implications from the most abstract principles in biology, all warnings notwithstanding.

The naturalistic fallacy is, for humans, remarkably natural. For instance, when an evolutionary biologist describes forced mating as a potential adaptive strategy, he can warn against the naturalistic fallacy page after page, but few readers will even

notice; most will be outraged because they think he approves of rape. His protests that he said no such thing will be ignored.

While such readers may be illogical, their reactions reflect important human tendencies. They intuitively recognize that describing a human behavior as a “normal” adaptation will lead many to conclude that the behavior is right, or at least not wrong. For instance, some young men, upon learning that natural selection has shaped organisms to maximize reproduction, change their personal sexual behaviour dramatically. I have also observed several people who changed their behavior after learning that relationships are mutually beneficial exchanges in which the maximum payoff goes those who can best deceive others. They changed not only their view of relationships, but their actual relationships; previously secure close partnerships became much more difficult. And then, of course, there is the dire history of people leaping from the fact of natural selection to justifications for eugenics and even genocide. Human views about the origins and functions of the moral capacities have tangible effects on behavior. Caution is warranted.

With this background, we can ask what neuroscience and evolution offer to understanding morality and immorality. The simultaneous focus in this book on psychopathy and normal moral capacities is particularly useful. Medicine has consistently found it difficult to explain abnormal conditions until both the normal mechanisms and their functions are clear. Conversely, studies of pathology often offer the best evidence about the functional significance of a trait. If you want to know what the thyroid gland is for, clues come from observing what happens when the thyroid gland is missing or malfunctioning. If you want to understand the benefits of moral capacities, study individuals who lack them.

Understanding the moral capacities requires two kinds of knowledge, evolutionary and proximate. They address fundamentally different questions (Dewsbury, 1999; Tinbergen, 1963). A proximate explanation is about how a mechanism works. Neuroscience offers proximate explanations at a low level. Psychology offers proximate explanations about morality at a higher level. Evolutionary explanations are different. They address why the mechanisms exist at all, in terms of selection and other evolutionary forces that account for the mechanism being the way it is. This is usually described as “the function” of a trait (although that often turns out to be too simple). Proximate and evolutionary investigations can inform each other, but they are about different questions.

Evolution

An evolutionary explanation of how moral capacities have increased fitness is the essential foundation for understanding morality. For the purposes of this book, the most important conclusion is that this foundation is still under construction. I have written much about this (Nesse, 2006), others have devoted their lives to it (Hammerstein, 2003; Katz, 2000) and this volume contains a comprehensive review (van Veelen in this volume). While much remains to be done, a rough framework is in place.

As most readers will know, naïve group selection seemed sufficient to explain altruism and morality until Williams pointed out its deficiencies (Williams, 1966), and Hamilton (Hamilton, 1964) and Trivers (Trivers, 1971) offered alternative explanations of kin selection and reciprocity, respectively. A vast amount of research since then has framed a general solution (Hammerstein, 2003). In very broad brush strokes, the vast majority of cooperative behavior in animals can be explained by kin selection or mutualisms. Well-documented examples of reciprocity in animals turn out to be rare (Stevens, Cushman, & Hauser, 2005), with the exception of our species. For humans, trading favors is at the center of life. We have emotions shaped to cope with the situations that routinely arise in reciprocity relationships (Nesse, 1990). Extraordinary social institutions enforce agreements, thus allowing vast social complexity.

Despite dozens of issues still on the table, a general explanation for moral capacities that facilitate exchange relationships is within reach. Skill in managing such relationships brings a net gain, and so selection should shape tendencies to do what works. That means paying close attention to who you are dealing with, and it usually means following rules. Explaining altruism beyond reciprocity and kinship (for instance, helping a dying friend), is more difficult. One approach is to explain such altruism away as self-deception or mistakes, another is to attribute it to group selection or cultural influences. I have previously argued that a capacity for commitment (in the economic game-theory sense of the word) can shape capacities for communal relationships that explain some aspects of altruism and our moral capacities. I still think that is important, but it leaves much unexplained.

Finally, I found articles by Mary Jane West-Eberhard (West-Eberhard, 1979; West-Eberhard, 1983) that offered a new perspective. In the late nineteen seventies she discovered that extraordinary social traits can result from the same kind of runaway selection that shape extraordinary sexually dimorphic traits, like peacock tails. The only difference is that the fitness benefits come not from being chosen as a mate, but from being chosen as a social partner. In the course of evolutionary history, once personal relationships began yielding a selective advantage, individuals who chose better partners began to gain an advantage. However, getting the best partners is not merely a matter of choosing, it depends more on being preferred as a partner. Individuals therefore display resources they can offer to their partners, and personal and moral characteristics that make them desirable partners, such as generosity and honesty. My paper, reprinted in this volume, unites this fundamental idea with modern mathematical models and findings from human social science, to argue that runaway selection based on partner choice can explain human moral and other social capacities that are otherwise inexplicable (Nesse, 2007).

One particularly interesting aspect, not developed in the article, is how social selection can explain why we value certain diverse personal characteristics as “virtue.” Recent sophisticated social science methods have revisited and confirmed long-recognized virtues such as bravery, creativity, wisdom, persistence, integrity, vitality, love, kindness, social intelligence, fairness, forgiveness, humility, gratitude, hope, and humor (Peterson & Seligman, 2004). How do all of these characteristics come together to be recognized as virtues? I suspect it is because they are the

characteristics we want in our partners. And, because we want to be valued as partners, they are also the traits we seek to display, and to live up to. They are products of social selection. Their unity may arise, not from a grand unifying philosophical principle, but from their origins in social selection for tendencies to choose, and to be, excellent relationship partners.

Evolution and Pathology

The framework of Darwinian medicine can be useful to analyze the evolutionary origins of presumably abnormal states, such as antisocial personality disorder (Nesse & Williams, 1994). Is it a disorder created only in modern environments, a product of infection, a tradeoff, a constraint, or is it an adaptation? The first question is whether it has had some kind of utility, but it is essential to keep all the alternative hypotheses on the table and not to jump to one conclusion.

Linda Mealey has argued that sociopathy might be a frequency dependent alternative strategy that gives a selective advantage when it is rare (Mealey, 1995). She notes a variety of supportive evidence, including the additional matings garnered by some psychopaths, however it is important to note several reasons why the hypothesis is not widely accepted.

Most alternative strategies are mating strategies, such as those used by dominant and subordinate male orangutans. Other morphs, such as benthic and limnic morphologies in fish, are alternatives for living in different ecological niches. These alternative strategies need not be associated with genetic differences. For instance, many fish change sex depending on the social environment. Such facultative adaptations, shaped by natural selection, monitor the environment and express one body type or another, depending on the situation. Locusts change from solitary to swarming morphs depending on the circumstances. The difference need not be categorical; early exposure to heat in infancy increases the number of sweat glands.

These principles may be useful for understanding antisocial personality disorder. It is hard to see the benefits of a genetically determined psychopath behavioral morph, when more flexible regulation would be more efficient. Why be stuck playing one strategy when flexibility is superior? Furthermore, substantial evidence now shows that genetic tendencies to sociopathy are not deterministic, they interact with early events to cause the disorder in some individuals. For instance, Caspi et al. found that rates of conduct disorder and criminal conviction increased dramatically with exposure to child abuse in all genotypes, but the increase was greater in those with low MAOA activity (Caspi et al., 2002). This suggests considering antisocial personality as an alternative strategy that emerges depending on early experience.

A more basic question is whether antisocial personality disorder is one condition, multiple related conditions, or positions on a continuum. Experience talking with psychopaths reveals their enormous diversity. Some use violence to get what they want. Others never use violence, but manipulate others, and get their greatest

pleasure from deceiving others, not from what they get out of the deception. Others have extraordinary seduction skills that allow them to get what they want, and then abscond. Others are simply socially incompetent; they cannot manage relationships, and they flounder in all kinds of ways. And, of course, others are simply shrewd political manipulators who become powerful leaders. Despite this observed variation, a review of five studies of antisocial personality disorder, finds four that support a view of antisocial personality as a distinct category instead of a dimension (Haslam, 2003).

This brings up the question of why such diverse characteristics as low empathy, impulsivity, using violence, and inability to have close relationships should occur together so reliably. The most obvious possibility is that all aspects arise from a common proximate cause, perhaps impulsiveness, or a low ability to learn from punishment. Another possibility is that they occur together because they are all useful aspects of a strategy for social influence. This could reflect a frequency dependent genetic strategy, as Mealey proposed, but there are several alternatives. They could also occur together as parts of a facultative adaptation that emerges in response to certain early experiences. However, they could also merely reflect what people fall back on when some defect in the cognitive and emotional apparatus makes normal social relationships impossible. Etiological heterogeneity is likely (Silberg, Rutter, Tracy, Maes, & Eaves, 2007) and there is no need to posit just one kind of deficit. Some might lack empathy, others may be unable to learn from punishment, others may simply be too impulsive to be reliable relationship partners, others may simply believe that others are untrustworthy. If a person is, for whatever reason, unable to create and benefit from ordinary social relationships, he or she will fall back to simpler strategies. Early experience with using violence and deception to manipulate others soon results, by simple learning, in more and more effective psychopaths who are locked into one strategy of social influence. The coherence of the syndrome may arise not from within, but from doing what works when you are incapable of maintaining and benefitting from enduring social relationships.

Neuroscience

Several chapters in this book demonstrate that moral decision making and moral emotions arise from brain mechanisms. Of course, we have long known that this had to be true. Nonetheless, because we are all innate dualists (Bloom, 2004), the simple fact can still seem shocking.

The next task is to find out what parts of the brain carry out moral tasks. Is one locus specialized for the task? Is there a circumscribed module to take care of it? As has been the case for other capacities, from language, to pain, to emotion, moral tasks are not processed in any one location. They may even be handled in different loci by different people. Several chapters in this book take on the challenge of trying to discover where the brain processes moral information. They amply demonstrate that these tasks are not carried out everywhere, but also that they are not carried out by a specific locus; they are carried out in diverse regions that are hard to specify.

It is disappointing that we cannot point to one brain locus, and say “morality happens here.” However, what we observe is exactly what an evolutionary perspective leads us to expect. A few very specific responses, such as vomiting and panic, have functions so specific and universally essential that they have been conserved for tens of millions of years; they have specific loci devoted largely to managing their expression. Equally old tasks that are not so tightly constrained, such as balance, are more distributed. New tasks, such as language, have been grafted onto existing structures in whatever way works, resulting in a hodge-podge of loci and connections.

This evolutionary view is very different from the massive modularity that is often associated with evolutionary psychology (De Schrijver in this volume). From my perspective, it is important to recognize that specific kinds of situations have posed the adaptive challenges that shaped brains with capacities for moral reasoning. The resulting mechanisms deal effectively with those situations. However, this by no means implies that selection would shape separate mechanisms to deal with each situation. On the contrary, we should expect modules with massive overlap in their arousal, processing, and output, and in the brain loci that mediate their functioning.

Moral capacities are very recent and very nonspecific. They require input of many kinds from many sources and outputs to many effectors. Selection shaped them by acting on relevant variation wherever it was available to co-opt old structures to new uses. For instance, disgust is ancient and has obvious adaptive utility – it motivates avoidance of pathogens (Curtis & Biran, 2001). Individuals with even a slight tendency to experience disgust after betrayal would avoid the betrayer. In just a few tens of thousand more years, it should not be surprising that moral violations arouse the same brain areas aroused by disgust (Greene & Haidt, 2002). Similarly, see Chapter 2 about how communal relationships and the moral emotions that sustain them seem to be have arisen from the mother infant attachment system (Moll & Oliveira-Souza in this volume). Both examples seem likely to be correct. They illustrate how evolutionary thinking can help inhibit tendencies to think of the brain as a machine with newly minted modules for each challenge, and how it can help us to accept the messy reality of functions carried out by multiple interconnected multifunctional loci.

Conclusion

Evolutionary analyses to understand the origins of moral capacities are coming along, but no one thesis is dominant at this point except for the general conclusion that natural selection has shaped capacities for coping with the situations that arise in reciprocity relationships, and additional moral capacities that make communal relationships possible.

Even at this stage, however, an evolutionary perspective can help to guide neuroscience research about antisocial personality disorder by encouraging attention

to how new functions have been grafted onto structures with multiple other functions, and attention to likely constraints that make such systems vulnerable to failure. Moral capacities are evolutionarily new and almost completely restricted to humans. This means that the substantial genetic variation in moral traits may best be explained because the phenotype is in transition. A related possibility is that optimum may vary markedly across groups and times. Even in a stable setting, fitness may be about the same across a wide range of the distribution.

What trait? Social selection shapes extraordinary concern about what others think about us, and motivations to please others. The benefits of such tendencies may explain why social anxiety disorders are vastly more common than psychopathy. The costs of excess social sensitivity are, however, large. It seems entirely possible that reproductive success will be roughly the same for individuals across a wide range of the distribution. Our expectation that there is some sharp peak that defines “normal” may be incorrect. This does not sit well with our human wish to define categories and declare some normal and some abnormal. However, it may reflect a more realistic view that can help us better understand morality and immorality.

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Runaway Social Selection for Displays of Partner Value and Altruism

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The discovery of evolutionary explanations for cooperation is one of the great achievements of late 20th century biology. As most readers know, benefits to the group rarely explain tendencies to help others (Williams, 1966; Dawkins, 1976), benefits to kin explain altruism in proportion to the coefficient of relatedness (Hamilton, 1964), and mutual benefits and reciprocal exchanges explain much cooperation between nonrelatives (Trivers, 1971). Subsequent theoretical and empirical studies have blossomed into a body of knowledge that can explain much social behavior (Wilson, 1975; Trivers, 1985; Dugatkin, 1997; Alcock, 2001; Hammerstein, 2003).

Controversies continue, however. Some arise from a profusion of models for cooperation that use inconsistent terminology and that tend to emphasize one explanation when several may apply (Frank, 1998; Hirshleifer, 1999; Hammerstein, 2003; Lehmann & Keller, 2006; Nowak, 2006; West, Griffin, & Gardner, 2007). Other controversies reflect impassioned debates about human nature (Midgley, 1994; Wright, 1994; Ridley, 1997; Segerstråle, 2000; de Waal, Macedo, Ober, & Wright, 2006; Dugatkin, 2006). However, some controversies persist because no explanation seems entirely satisfactory for some phenomena, especially human capacities for altruism and complex sociality.

While kin selection and variations on reciprocity explain most human capacities for cooperation, some observations don't fit the usual models. In behavioral economics laboratory experiments, and in everyday life, people tend to be more altruistic than predicted (Gintis, 2000; Fehr & Rockenbach, 2004; Brown & Brown, 2006; de Waal et al., 2006). They also tend to punish defectors even when that is costly (Henrich & Boyd, 2001; Boyd, Gintis, Bowles, & Richerson, 2003). People follow rules and they are preoccupied with morals and mores, monitoring and gossiping about even minor deviations (Axelrod, 1986; Katz, 2000; Krebs, 2000;

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de Waal et al., 2006). Perhaps most interesting of all, close friends take pains to avoid making exchanges explicit because calling attention to them harms relationships (Batson, 1991; Mills & Clark, 1994; Dunbar, 1996; Tooby & Cosmides, 1996; Nesse, 2001, 2006; Brown & Brown, 2006). Friendships exist, but they remain in want of a satisfactory evolutionary explanation (Smuts, 1985; Silk, 2003).

This article argues that well-established models of social selection may explain how partner choice could shape extreme prosocial traits in humans. It begins by reviewing early descriptions of social selection (West-Eberhard, 1979, 1983) and more recent formal models that illustrate the value of calculating the fitness components from social selection separately from those that arise from the rest of natural selection (Tanaka, 1996; Wolf et al., 1999; Frank, 1998, 2006). Next, it reviews the recent recognition of the power of partner choice (Noë & Hammerstein, 1994) and connects these insights with recent models of how covariance of partner phenotypes can lead to runaway social selection (Tanaka, 1996; Breden & Wade, 1991). These lines of work come together with recent work on human altruism to suggest that the fitness benefits of being chosen as a partner may shape extreme displays of partner value, including capacities for genuine altruism, that are otherwise difficult to explain.

Social Selection

Social selection is the subtype of natural selection in which fitness is influenced by the behavior of other individuals (West-Eberhard, 1979, 1983; Wolf et al., 1999; Frank, 2006). Although well-established in biology, the term social selection is slightly problematic because epidemiologists use the same phrase to describe the entirely different phenomenon of some social groups having a higher proportion of individuals with some condition. For instance, the proportion of people with schizophrenia is higher in inner cities simply because many cannot afford to live elsewhere. Also potentially confusing is the idiosyncratic use of social selection as an alternative to sexual selection (Roughgarden, Oishi, & Akcay, 2006), when in fact it is a subtype. These potential confusions aside, social selection is the standard term for fitness changes resulting from the social behaviors of other individuals.

Sexual selection by female choice is the best known subtype of social selection. Female biases for mating with ornamented males select for more elaborate male displays, and the advantages of having sons with extreme displays (and perhaps advantages from getting good genes) select for stronger preferences (Grafen, 1990; Kokko, Brooks, Jennions, & Morley, 2003). The resulting positive feedback makes displays and preferences more and more extreme until genetic variation is exhausted, or until the fitness increase from more matings equals the fitness decrease from lowered competitive ability and earlier mortality (Andersson, 1994; Kokko, Jennions, & Brooks, 2006). Sexual selection is social selection because individual fitness is influenced by the choices and behaviors of other individuals. West-Eberhard made the point succinctly in one of the first papers on the topic:

Sexual selection refers to the subset of social competition in which the resource at stake is mates. And social selection is differential reproductive success (ultimately, differential gene replication) due to differential success in social competition, whatever the resource at stake.” (1979, p. 158).

Social selection arising from conspecific choices and behaviors has been described in detail (Crook, 1972; West-Eberhard, 1975, 1983; Tanaka, 1996; Wolf et al., 1999; Frank, 2006). Surprisingly, however, its full power is just now being recognized. The perspective of social selection shifts attention away from individual strategies in iterated exchanges, and towards the prior and larger fitness challenges of identifying the best available partners and doing whatever will get them to choose one as a partner. In formal models, this means partitioning the force of social selection resulting from the covariance of partner’s phenotypes separately from other forces of natural selection. Following Queller (1992) and Frank (1997), Wolf, et al. (1999) describe social selection by saying “factors other than one’s own phenotype may affect an individual’s fitness. . . individual variation in fitness can be attributed to variation in the value of traits expressed by an individual’s social partners.” (1999, pp. 255–256).

Building from Lande and Arnold’s model of sexual selection (1983), Wolf, et al. (1999, p. 256) partition relative fitness ω into one component from social selection and a separate component from the rest of natural selection: $\omega = \alpha + \beta_N z_i + \beta_S z'_j + \epsilon$ where β_N is the natural selection gradient, β_S is the social selection gradient, z_i is the trait in the individual and z'_j is a covarying trait in the partner (the prime sign indicates that the trait is in the partner, α is fitness uncorrelated with the traits, and ϵ is error). They then derive a generalized phenotypic version of Hamilton’s rule to show that selection favors an altruistic trait z_{ij} whenever $\frac{C_{ij}^{ij}}{P_{ii}} \beta_S + \beta_N > 0$, where C_{ij}^{ij} is the phenotypic covariance between the trait in the individual and the partner, and P_{ii} is the character’s variance. Here, β_N is the selection cost for an altruistic trait (and will therefore be < 0), and β_S is the benefit to the partner (which will be > 0), so the altruistic trait will be selected only if its covariance with the associated trait is large compared to the trait’s variance. The model, very similar to Frank’s (1997, 1998), and also drawing on Fisher and Price, is based on phenotypes and does not require covariance of genes within individuals. Partner choice creates phenotypic covariance that can shape extreme traits such as displays of one’s value as a partner. How far will social selection push such traits at the expense of other components of natural selection? An answer to this important question requires detailed analysis of social selection by partner choice.

While all social behavioral tendencies can be interpreted as products of social selection because they involve choice by other individuals (Wolf et al., 1999; Frank, 2006), the emphasis here is on forces of selection that arise from choices about relationship partners and group membership. If potential partners or group members vary in resources and tendencies to reliably bestow them on close partners, then a preference for resource-rich selectively-altruistic partners will give a selective advantage. Being preferred as a partner gives fitness advantages because it gives more possible partners to choose from (Noë & Hammerstein, 1994). This will select

for displays of resources and selective altruism that reflect an individual's potential value as a partner.

The nonrandom association of individuals with extreme displays and those with strong preferences can result in runaway social selection that increases both traits to extremes that decrease other fitness parameters (Breden & Wade, 1991; Tanaka, 1996; Wolf et al., 1999). This model differs from sexual selection because in most cases preferences and displays will both be present in the same individuals. Also, benefits to others pay off not only directly, but also because benefits to partners eventually result in benefits to the self via interdependence (Rothstein, 1980; Humphrey, 1997; Brown & Brown, 2006). At equilibrium, many individuals will be presenting and assessing expensive displays in a competition that results in partnerships between individuals of similar partner value.

In sexual selection, runaway occurs only when the covariance of the trait and the display is greater than the viability decrease from the display. At equilibrium, further increases in female preference would lower fitness because of decreased viability of sons (Kokko et al., 2006). However, "even small changes in female behavior (which cost little) can generate strong selection when a male's fitness depends primarily on his mating success." (Kokko et al., 2006, p. 59). In selection for social partners, the cost of choosing partners with extremely high value has little or no disadvantage comparable to the disadvantage experienced by females who chooses mates with the most extreme displays. Displays of partner value will, therefore, continue under directional selection until their marginal benefits impose equal costs to other fitness components, such as ability to accumulate material resources. Thus, social selection for partners can, like sexual selection, explain extremely costly traits.

In a model of social selection that emphasizes signaling submission and real fighting ability, Tanaka (1996) addresses the possibility of runaway social selection more directly. As in the Wolf, et al. model, fitness is partitioned into components from social selection that are distinct from the rest of natural selection in order to assess where the equilibrium for a signal lies. That point often is reached, he concludes, by runaway selection that quickly arrives at the equilibrium where the marginal benefits of further increasing the signal are balanced by its direct costs. Crespi (2004) has argued that such positive feedback cycles are much more common in nature than is usually recognized. Deception and cheating have been major themes in reciprocity research, and they apply in social selection models, but their effects are limited by inexpensive gossip about reputations and by the difficulty of faking expensive resource displays (Tanaka, 1996).

Social Selection in Nature

If the above models are correct, then examples of non-sexual social selection should be observed in the natural world. Some examples of traits shaped by preferences in one species for displays in another species illustrate runaway selection without genetic covariation in the same genome. As Darwin noted (1871), flowers have elaborate and diverse forms because they compete to satisfy pollinator preferences. Flowers preferred by pollinators contribute more genes to future generations, so

floral displays become increasingly extravagant until the marginal benefits from attracting more pollinators are matched by costs to other aspects of fitness, such as investment in leaves and roots (Armbruster, Antonson, & Pélabon, 2005). Benefits can also come from not being chosen. Staying near the center of a selfish herd is shaped by predator preferences. Stotting protects gazelles because it is an honest signal of vigor that discourages predators from useless chases.

Signals between members of the same species are shaped by the same mechanisms (Grafen, 1984; Bradbury & Vehrencamp, 1998). Social coordination signals are ubiquitous. For instance, a bird on a nest makes distinctive movements to signal to its partner that it is ready to trade roles. The signal benefits both parties, so there is no selection for an extreme signal. In competitive situations, amplified signals are common (Tanaka, 1996). When a wolf bares its throat to signal yielding in a fight, both parties benefit by avoiding the danger of an escalated fight; a prominent submission display that creates real vulnerability pays off by avoiding useless fighting. Status displays in lieu of a fight are likely to be extreme because only expensive honest signals will influence the competitor. Note that such signaling behaviors give benefits only because they interact with the phenotypes of other individuals who have been primed by selection to be influenced.

Some examples, such as males competing for a territory, blur the boundary between sexual and other social selection. Others arise more clearly from nonsexual social selection, such as the huge brightly colored beaks of both male and female toucans. They do not result from sexual selection; non-social toucan species have less exaggerated and more sexually dimorphic beaks. They are more likely honest signals of ability to defend a nesting territory (West-Eberhard, 1983). Bright coloration in both sexes is also prominent in territorial lizards and some mammals, especially lemurs. Social selection has also been proposed as the explanation for bright coloration of reef fish. West-Eberhard offers a wealth of examples, and reasons why species recognition hypotheses are insufficient (1983). She also notes that Wynne-Edwards (1962) provides additional examples, even if he was wrong about how selection shaped them. This is especially important because it highlights the power of social selection to account for phenomena that might otherwise appear to be products of group selection. While the sources of female ornamentation remain an active research focus, a recent review endorses the importance of social selection:

Almost 20 years ago, West-Eberhard argued that monomorphic showy plumage was associated with aggressive social displays (over territories or other resources) by both sexes. Her argument was supported by examples from several taxa including toucans, parrots and humming birds. West-Eberhard's suggestions resulted in surprisingly little empirical research in the following years. However, among published studies, most seem to support her view (Amundsen, 2000, p. 151).

Domestication

Domestication illustrates how social preferences can shape profoundly prosocial traits. It requires no conscious breeding, only preferences that influence fitness among individuals from the other species who vary on traits that matter to humans

(Price, 1984; Diamond, 2002). For instance, wolves with less fear of humans and lower levels of aggression were able to, and allowed to, stay closer to ancestral human camps where the fitness value of food scraps was a domesticating selection force. In turn, those humans who had tendencies to be altruistic towards dog-progenitors received fitness benefits – initially warnings of danger, but later, help in the hunt and protection. This process selected for genes that increase human altruism towards dogs, and it shaped dogs who behave in ways that please humans enormously.

Humans also show many characteristics of being domesticated – low rates of aggression, increased cooperation, eagerness to please others, and even changes in bone structure similar to those characteristic of domesticated animals (Leach, 2003). It seems plausible that humans have been domesticated by the preferences and choices of other humans. Individuals who please others get resources and help that increase fitness. Aggressive or selfish individuals get no such benefits and are at risk of exclusion from the group, with dire effects on fitness. The result is thoroughly domesticated humans, some of whom can be enormously pleasing.

This process does not depend on the success of the group. Instead, individuals constantly make small self-interested social choices that shape the behaviors of others who learn to do whatever works. The resulting effects on fitness shape the species by social selection. This process offers a dramatic example of a Baldwin effect, in which learning shapes adaptive behavior patterns that create new selection forces that rapidly facilitate better ability to exploit the new niche (Dennett, 1995; Laland, Odling-Smee, & Feldman, 2000; Weber & Depew, 2003; West-Eberhard, 2003; Ananth, 2005). Once the benefits of relationships increased above a crucial threshold, they created a newly complex social environment where individuals with special social skills got increasing fitness advantages shaped more extreme cognitive and prosocial traits (Humphrey, 1976; Byrne & Whiten, 1988; Alexander, 2005).

Herbert Simon, in a 1990 article on “social selection and successful altruism,” described how selection for “docility” could give rise to behaviors that benefit others more than the self. Simon defined docility as, “persons who are adept at social learning who accept well the instruction society provides them” (p. 1666). His model is based on the fitness benefits of general social learning, and the assumption that “limits on rationality in the face of environmental complexity” result in individuals behaving altruistically for the good of society without recognizing the “tax” they are paying. In contrast, the model developed in this article views altruism as a result of the fitness benefits of social selection, not as a result of cognitive constraints.

Social Selection for Cooperation

Indirect benefits to kin are one powerful force that shapes conspecific cooperation. Ability to recognize kin, and preferences for helping them, give benefits to genes in kin that are identical by descent to those in the helper (Hamilton, 1964; Dugatkin, 1997; Frank, 1998; Queller & Strassmann, 1998; West, Pen, & Griffin, 2002). This

process has been described and studied so extensively that there is no need to repeat the details here. One subtype, “green-beard effects” has been controversial, but it now appears that selection does sometimes shape kinship cues that facilitate kin altruism (Queller, Ponte, Bozzaro, & Strassmann, 2003). Phenotype variability can also be shaped by social interactions involved in reproductive competitions, at least in wasps (Tibbetts, 2004).

Preferences for helping nonrelatives who will help in return are also obviously valuable (Trivers, 1971). The challenge is how to get the benefits of trading favors without being exploited (Krebs & Dawkins, 1984; Alexander, 1987; Cosmides, 1989; Fehr & Fischbacher, 2003). Following Price (Frank, 1997) and Queller (1992), Frank (1997, 2006) points out that such cooperation can be modeled as correlated behaviors, an information problem equivalent to that of kin selection. In kin selection, a behavior increases inclusive fitness if its cost to the self is less than the benefit to the other times the coefficient of relatedness, r . In correlated behaviors, the cost is the direct effects of the behavior on the individual’s fitness, the benefit is the indirect benefit from others (holding constant individual behavior), and r reflects the similarity of other’s behavior, that is, the information an individual has about benefits others will likely offer. Both kin selection and correlated behavior can thus be analyzed by partitioning fitness into direct costs, indirect benefits, and a scaling factor that reflects relatedness in the former case, and information about other’s anticipated behavior in the latter (Frank, 1997; Wolf et al., 1999).

The iterated prisoner’s dilemma has long been the dominant model for cooperation based on reciprocity (Axelrod, 1984; Sigmund, 1993; Axelrod, 1997). In this model, the maximum joint benefit for two players comes from repeated cooperation, but an individual can get a greater payoff from defecting on any move when the other cooperates. Tit-For-Tat (starting with a cooperative act and then doing what the other person did on the previous move) is a remarkably robust strategy that nicely models some human interactions. The tractability of models based on the prisoner’s dilemma has fostered scores of valuable studies (Axelrod, 1997).

It is less clear, however, that prisoner’s dilemma models accurately reflect the kinds of trait variation on which selection acted to create capacities for social cognition. In most studies, anonymous agents are randomly paired, information is only about prior behavior with one agent or the sum of all agent’s behavior, the same algorithm is used for interactions with all other players, and only two outcomes are possible, cooperate or defect. Reputation and punishment have increasingly been added to such models (Fehr & Fischbacher, 2003; Axelrod, Hammond, & Grafen, 2004; Henrich et al., 2006). However, few reciprocity models have all of the ingredients that are important to human cooperation in close relationships: reputation, communication, agreements, promises, threats, third party enforcement, and especially, opportunities to use extensive information to choose partners from a selection of possibilities (Kitcher, 1993; Hammerstein, 2001; Nesse, 2001; Noë, 2001). While variations in tendencies to cooperate or defect in discrete interactions with rapidly shifting partners certainly create selection forces, they explain only some aspects of some human relationships (Fehr & Henrich, 2003; Barclay & Willer, 2007). Nonetheless, such models have been a boon for the study of cooperation.

Another difficulty is that the kinds of reciprocal exchange modeled by the prisoner's dilemma seem to be rare in nature. Most apparent examples of reciprocity identified by field research now appear to be better explained by kinship or mutual benefits (Connor, 1995; Stevens, Cushman, & Hauser, 2005). Cooperative hunting is a prime example. Participants all gain, so defection does not pay. Impala grooming is a reciprocal exchange, but of the most minimal kind. Grooming bouts are traded back and forth in parcels so small that the example blurs the border between reciprocity and mutualism (Connor, 1995), although grooming may be tradable for other resources (Manson, Navarrete, Silk, & Perry, 2004). Another example, previously thought to exemplify reciprocal exchange between nonrelatives, is vampire bats sharing blood with others who did not succeed in that night's hunt (Wilkinson, 1984). However, it turns out the sharing almost always is between kin. Coalitions of male baboons were also thought to demonstrate reciprocity, but on reexamination, the males do not share mating opportunities to any great extent. A review by Stevens, et al. (2005) assesses the evidence for reciprocity in nature and concludes that there are few examples, perhaps, they say, because most animals have severe capacity constraints for memory and cognition.

Where reciprocal helping does exist, it is usually maintained by systems for assessing potential partners or withdrawing resources from defectors (Sachs, Mueller, Wilcox, & Bull, 2004). Parceling, as in reciprocal grooming, distributes resources in small packets so defection is not an issue (Connor, 1995). Another strategy is to distribute resources selectively depending on the behavior of others. For instance, yucca plants abandon flowers with too many moth larvae. This can be viewed as a punishment that selects for moths who limit egg deposition. However, abandoning the flowers with too many larvae is in the direct self-interest of the yucca plant, and this makes it advantageous for moths to limit the number of eggs laid in any one flower.

Image scoring (Nowak & Sigmund, 1998; Wedekind & Milinski, 2000) and other reputation-based strategies such as indirect reciprocity (Alexander, 1987), offer information about an individual's reliability as a partner and can lead to mutually profitable exchanges even in the absence of repeated interactions (Riolo, Cohen, & Axelrod, 2001). This is not the place to analyze the diversity of cooperation models, but it is important to recognize that delayed reciprocal exchange of resources is as rare in other animals as it is ubiquitous in humans. Furthermore, human cultures vary substantially in their levels of individual cooperation, with much of the variance attributable to variations in the patterns of economic exchange (Henrich et al., 2005), further demonstrating that human cooperation strategies are marshaled to suit the circumstances.

The role of partner choice in facilitating cooperation has long been recognized (Bull & Rice, 1991), but has been emphasized only recently (Noë & Hammerstein, 1994; Noë, 2001; Sachs et al., 2004). When there is choice, potential partners must compete in markets that change the dynamics of cooperation. Between-species partner choice is illustrated by symbioses in which the slower-evolving organism selects among individuals in a faster evolving species to get the most valuable partners, for instance, the plant symbioses with bacteria and fungi (Simms & Taylor, 2002;

Kummel & Salant, 2006). Choice of conspecific partners may be far more powerful (Roberts, 1998; Noë & Hammerstein, 1994).

Social Selection for Prosocial Traits in Humans

The possibility that social selection shaped human capacities for altruism and complex sociality was suggested in West-Eberhard's seminal publication on the topic (1979, p. 228):

It is tempting to speculate that the explosive evolutionary increase in the proto hominid brain size, which had the appearance of a "runaway" process, was associated with the advantage of intelligence in the maneuvering and plasticity associated with social competition in primates.

The complexity of the social environment is widely recognized as a selection force likely to be important for explaining human social abilities (Humphrey, 1976; Alexander & Borgia, 1978; Alexander, 1979; Byrne & Whiten, 1988). The full implications for human prosocial traits have yet to be developed, although one wide-ranging treatment suggests that social selection may have enormous scope for explaining human capacities for art and literature, as well as capacities for intelligence and cooperation (Alexander, 2005).

A closely related model for the evolution of human altruism is based on sexual selection. Geoffrey Miller (2000, 2007) has suggested that sexual selection may account for many extreme human cognitive and behavioral traits that are otherwise difficult to explain, especially altruism. He cites evidence that both women and men prefer to marry kind reliable partners, giving a fitness advantage via sexual selection to individuals of both sexes with these heritable personality traits. Sexual selection could thus shape extreme altruism. This potentially important hypothesis has not been emphasized in recent literature, perhaps because it is difficult to study. Miller (2000) acknowledges that other forms of social selection may be important, but mostly, he says, "because they change the social scenery behind sexual selection."

Mate choices create potent selection forces, but so do choices of relationship partners. The fitness benefits from choosing social partners are more distant from direct reproduction, but they can influence fitness nearly every day and at all ages. If partnerships yield a net gain for both parties, then fitness increases with the increase in the number of others who want you as a partner, at least for the first few partners. If partners vary in value, then fitness will be increased by behaving in ways that increase the number of others who want you as a partner (Noë & Hammerstein, 1994). A good way to increase the number of available number of partners is to advertise, and to usually provide, more benefits than others can or will provide (Roberts, 1998; Barclay & Willer, 2007; Hardy & Van Vugt, 2006).

Such "competitive altruism" has been the topic of several descriptions and studies (Roberts, 1998; Barclay & Willer, 2007; Hardy & Van Vugt, 2006). The latter two studies are especially germane because they model and provide data that demonstrate competitive altruism in humans. Competitive altruism gives an advantage

when extreme generosity results in disproportionate payoffs from pairing with the best partners. In Barclay and Willer's study using a prisoner's-dilemma-like task, generosity levels increased dramatically when participants knew their behaviors were observable and could be used by others choosing partners. The effect was robust even though the experiment was anonymous. Hardy and Van Vugt also demonstrated increased altruism when behavior is observed, and they found that the most altruistic individuals gained the highest status and were preferred as partners, thus gaining benefits.

The resulting positive feedback process can shape costly displays, and preferences for partners who present such displays. Displays of resources, talent and other indicators of partner value are prominent aspects of human cultures (Barkow, 1989; Dunbar, Knight, & Power, 1999; Miller, 2000; Schaller & Crandall, 2003; Alexander, 2005). Conspicuous consumption, from potlatches to Rolexes, has been interpreted as wasteful status displays (Veblen, 1899), but such displays not only entice mates, they also advertise an individual's desirability as a relationship partner or a group member. Competitions in such displays reward only the most extreme and remarkable performances and creations (Veblen, 1899; Frank, 1999; Alexander, 2005).

People advertise their reputations as much as their resources, and displays of moral character are an equally impressive aspect of human cultures (Katz, 2000). Reputation display competitions may be important for explaining human moral capacities and altruistic behaviors that are not reliably reciprocated. Recent models suggest that altruism itself may be an honest advertisement based on the handicap principle (Gintis, Smith, & Bowles, 2001; Pilot, 2005; Hardy & Van Vugt, 2006; Barclay & Willer, 2007).

Strong reciprocity is closely related (Gintis et al., 2001). As Fehr and Henrich put it (2003, p. 57), "The essential feature of strong reciprocity is a willingness to sacrifice resources in both rewarding fair behavior and punishing unfair behavior, *even if this is costly and provides neither present nor future economic rewards for the reciprocator.*" They argue that this apparently "excess" altruism is not a mistake, but an adaptation that arises because even small amounts of conformist transmission give advantages to cooperate-punish strategies that result in their spread in cultural groups. The previous argument about the Baldwin effect and emergent forces of selection in groups is similar, but focuses more attention on behaviors at the level of the individual. Prior work on the evolution of capacities for commitment (Nesse, 2001) is also related, although commitment strategies rely more on intensive communication of threats and promises, and ways to make them believable even when fulfilling the commitment would not be in the actor's interests. As noted already, research on cooperation is vulnerable to confusion because it probably is shaped by multiple selection pressures that are hard to disentangle.

The assortment that brings cooperators together need not be based on recognition or identity tags; simple environmental or partner preferences are sufficient (Pepper & Smuts, 2002; Pepper, 2007). Any mechanism that associates cooperators gives advantages to those with prosocial traits (Wolf et al., 1999; Frank, 2006). The results of such selective association of cooperators can be framed as trait-group selection (Wilson & Sober, 1994), but such models are very different from old group

selection, so to prevent confusion “an alternative is to state as simply as possible what they are – models of nonrandom assortment of altruistic genes” (West et al., 2007, p. 11).

The opportunity to choose from a variety of partners, and the possibility of negotiating contracts and prices, suggests applying market models to the problem of cooperation (Noë & Hammerstein, 1995; Hammerstein, 2001; Noë, Hooff, & Hammerstein, 2001). Consumers and producers, whether humans, other animals, plants or fungi, select among available partners based upon their utility, availability, and price. Replacement of cheaters with more profitable partners exerts a powerful selection force for transaction quality and the ability to conceal and detect defection (Frank, 1988, Trivers, 2000). This shapes market efficiency and integrity, even to the apparently maladaptive extreme of guarantees that “the customer is always right.” Such guarantees are exploitable and costly, but competition for customers keeps them prevalent.

The argument that social selection shapes extreme traits for winning competitions for relationship partners can be readily expanded to encompass parallel processes at the group level. Individuals in groups assess the qualities of potential future members and admit those who offer the most while demanding the least. Conversely, prospective new members assess which group offers them the most at the least cost. The result is a sorting of individuals by their abilities to contribute resources, creating groups readily ranked in quality. However, because being a big fish in a small pond can payoff better than being a small fish in a big pond, the partner value of members will overlap between groups (Frank, 1985).

Skew theory (Reeve & Shen, 2006) may clarify the dynamics of individuals competing for resources other than access to reproduction in social groups. Individuals in groups should value new members proportional to their effects on group members’ ability to get resources. Potential members display both their resources and their willingness to share them. After an individual joins a group, the dynamics shift to those based on the costs and benefits of allowing a member to stay, and competition for allies and position within a group. Social selection from competitions to join the best groups may be more powerful than competition to be chosen as an individual partner, but the complexities make it wise to focus here on simpler partnerships.

It is important to note that the behaviors of individuals groups can create emergent forces of natural selection in groups that shape otherwise inexplicable traits such as genuine altruism, group loyalty and boundaries that define the in-group and devalue out-groups (Alexander & Borgia, 1978; Boyd & Richerson, 1985). Such forces may emerge reliably from individuals and partnerships pursuing their own interests. While such emergent selection forces would not exist without the group, they are very different from group selection in that they do not depend on the success of the group.

Models

Most models partition fitness effects into social selection and natural selection components, and describe how covariance between traits in associated partners can account for the strength of social selection (West-Eberhard, 1975; West-Eberhard,

Correlations of G with C: Fixed Partnerships

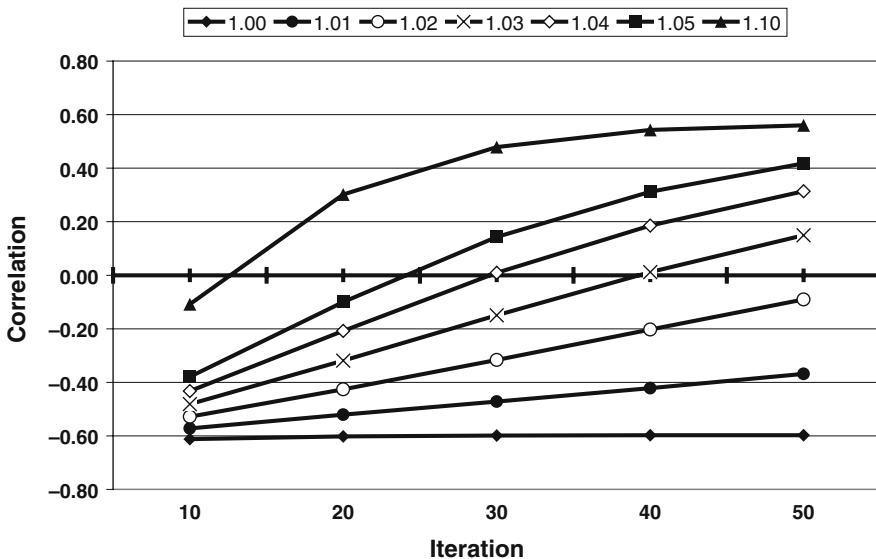


Fig. 1 Correlation of G with C for fixed partnerships over 50 iterations for six levels of R

1983; Tanaka, 1996; Wolf et al., 1999; Frank, 2006). It is difficult, however, for such models to describe the dynamic process of choosing repeatedly among many possible partners as a function of behaviors that change over time.

An agent-based shared-investment model may help to illustrate some of these processes. A simple initial model assigns each agent a randomly distributed generosity parameter, G, that ranges from 0.0 to 1.0. Each of 100 agents is endowed with capital, C=100. In each iteration, pairs of agents invest a percentage of their total resources, (G*C) and (G*C') respectively (the prime mark indicates the partner's parameters). Both partners receive a payoff equal to half of their total joint investment times R, the rate of return: $Payoff = R * ((G * C) + (G' * C')) / 2$.

If this model is run without sorting, agents remain in fixed pairs. The agent with a higher G does worse because it invests more than the partner on each move, but they share the payoffs equally. Despite the higher payoffs for the less generous agent in each pair, when all 100 agents are considered, more generous agents on average have superior payoffs as reflected in increasing correlations of G with C with each iteration. The correlation of G with C increases with each iteration. How fast it becomes positive depends on R. As shown in Fig. 1, when R=1.03, correlations become positive by iteration 40. For R=1.05 the correlation becomes positive at iteration 25, but reaches only 0.40 at iteration 50. When R=1.10, the correlation becomes positive at iteration 12 and approaches an asymptote of 0.60.

Model 2 is the same except that at each iteration the agents are sorted according to GxC, the total investment made on the previous move. This increasingly pairs

Correlations of G with C: Partner Choice

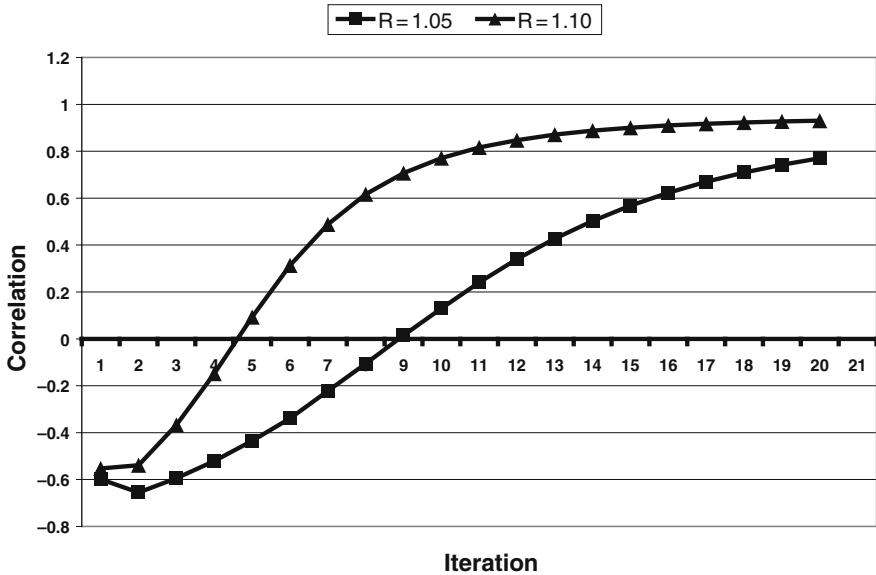


Fig. 2 Correlation of G with C given partner choice over 50 iterations for two levels of R

more generous agents as if each one were watching all others and pairing with the available partner who offers the best combination of resources and generosity. More generous agents still accumulate capital more slowly than their less generous partners, but the sorting process greatly increases the maximum correlation and how quickly it becomes positive. As illustrated in Fig. 2, $G \times C$ becomes positive at the 9th iteration if $R=1.05$, and at the 5th iteration if $R=1.10$. Both continue on to correlations much higher than in the model without partner choice.

These simple models illustrate how partner choice can shape increased generosity. The model could easily be elaborated by allowing reproduction as a function of capital accumulation, or by using a genetic algorithm to see what parameters are optimal and whether different subtypes of agents find evolutionarily stable alternative strategies. Such models could also use random normal distributions of R in order to study the influence of stochastic payoffs. It will be interesting to discover the optimal levels of generosity across different levels of other parameters and whether populations of agents go to a stable equilibrium or if they cycle. Future models also need to incorporate the possibility of deception, although continuing choice among known potential partners makes deception less important than in most reciprocity models. Social selection models lend themselves to investigations of how hierarchy influences cooperation.

The Invisible Hand

Adam Smith was preoccupied with finding explanations for sympathy (Smith, 1976 [1759]), and his followers argue that he would be dissatisfied with current evolutionary theories of altruism (Kahil, 2004). In his book on the moral passions, Smith mentioned the invisible hand only once, and this was with respect to the division of resources. The idea of the invisible hand seems equally germane, however, to the origins of moral emotions. Individuals pursue their interests by trying to attract the best possible partners. To succeed, they must offer to fulfill the wishes and expectations of potential partners at the lowest possible price. This usually requires carrying out many expensive actions that help and please others. Self-interested partner choice may be the invisible hand that shaped human capacities for sympathy.

Social exchange with partner choice gives rise to emergent forces of natural selection that can shape social traits far more sophisticated than generic sympathy. These forces should give fitness advantages to those who pay close attention to what others want, something very much like theory of mind. They could also shape empathic concern for the welfare of partners and strong motives to make reparations, not only for actual defections, but for even hints of possible lack of attention to the other's needs (Wu & Axelrod, 1995). And, they can shape love, spite, contempt and the whole range of social emotions (Nesse, 1990). Most globally, these social market forces shape desires to please others in general, and desires to avoid any cause of displeasure. Indeed, powerful internal mechanisms reward us for helping others (Brown, Nesse, Vinokur, & Smith, 2003), and cause guilt and shame when we cause others pain or disappointment (Gibbard, 1990).

Caveats and Conclusions

Several caveats and limitations should be kept in mind. First, as already noted, multiple mechanisms of selection shape capacities for cooperation. While this article emphasizes the effects of runaway social selection resulting from social partner choice, several other forces are involved, including sexual selection, the benefits of mutualisms, and plain reciprocity.

Second, and closely related, the fitness benefits of social selection are intimately involved with reciprocity and kin selection. In one sense this is not an issue. Other different perspectives, such as reciprocity and kin selection, can be modeled in a common framework. The social selection perspective is distinctive, however, because it shifts the focus of attention away from decisions to cooperate or defect and abilities to detect cheating, and towards the quite different tasks of selecting carefully among a variety of potential partners, trying to discern what they want, and trying to provide it, so one is more likely to be chosen and kept as a partner.

Reciprocity and social selection models of cooperation differ not only because they partition fitness effects differently, but also because social selection gives rise to runaway processes that can account for traits that decrease survival or competitiveness, such as extreme altruism. For the same reason, the benefits of

socially selected traits may come at the cost of increased vulnerability to serious mental disorders. For instance, rapid selection for complex social capacities may have pushed some traits close to a fitness “cliff-edge” beyond which lies catastrophic cognitive failure of the sort seen in schizophrenia (Nesse, 2004).

Social selection calls attention to the locus of selection’s action: heritable variations in social traits that influence abilities to get and maintain relationships with preferred social partners. Empathy, self-esteem, guilt, anger and tendencies to display moral traits and to judge others may be shaped directly by social selection. Instead of describing a stable equilibrium, social selection focuses attention on the dynamic process that shapes social traits.

Third, human nature is not unitary. Some people are profoundly prosocial, others lack all sympathy. Do individuals who lack sympathy have a genetic defect? Or, did they miss some early experience necessary to development of the capacity? Or, is sympathy a facultative trait expressed only in certain social circumstances? Or is selection for such capacities so recent that gene frequencies are changing rapidly? Or are they maintained in some frequency dependent equilibrium? (Mealey, 1995). These are important questions, as yet unanswered. While finding the mean values and distributions for any trait in any species is valuable, attempts to essentialize human nature are at odds with both observation of human variation and an evolutionary view of how human nature came to be.

Forces of social selection may also vary significantly between different groups (Henrich et al., 2005). Even within one society, different subgroups show different social patterns. It also seems possible that the benefits of partner choice may be much larger in some settings compared to others. For instance, if most economic activity requires little cooperation and no trading, then attending closely to other’s needs will be of little value as compared to a situation in which competitive presentations of self influence fitness strongly. High rates of narcissism may be a reliable product of certain social and economic structures (Lasch, 1979).

A related concern is whether the opportunities for partner choice have influenced fitness long enough to create forces of social selection sufficient to shape complex social traits. To find out will require anthropological data interpreted in this framework. The possibility that capacities for profound sociality arose from culture without influences from natural selection seems unlikely. Humans clearly have social capacities that are qualitatively different from other animals (Kitcher, 1993; Dunbar, 1998; Tomasello, 1999).

Finally, words hide all manner of imprecision that is revealed only by transforming them into mathematical statements. The mathematical models in this paper are rudimentary. Among other factors that need exploration are deception, different parameters for payoffs and noise, and the possibility that viscosity or other grouping mechanisms may maintain different equilibria.

No definitive experiment is likely to prove the role of social selection in shaping human capacities for cooperation, and, for the reasons just noted, cross-species comparisons will not be very useful. Nonetheless, just as a reciprocity models suggested looking for specialized cheater detection capacities, social selection models suggest looking for specialized capacities for determining what others want, for monitoring

whether one is pleasing them, and for presenting a social self that will make one desirable as a social partner. Of course, we already know quite a lot about theory of mind and the evolution of self-esteem (Leary & Baumeister, 2000), so to demonstrate that they were shaped by social selection will require predicting unnoticed aspects and looking to see if they are there.

In sum, partner choice can create runaway forces of social selection that may have shaped human prosocial tendencies and capacities for advanced social cognition that are otherwise difficult to explain. Whether this turns out to be correct awaits additional modeling, experiments, field studies, and further syntheses with the principles of microeconomics.

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