1 Introduction

Behavioral morality is the set of moral rules we attribute to people by virtue of their actions. Classical morality is the set of rules that philosophers and theologians consider that moral individuals are obliged to obey. The content of both behavioral and classical morality are contested, and the appropriate complex. This essay deals with behavioral morality alone.

Traditional social science embraces a rather straightforward understanding of the relationship between human biological evolution and morality. This is the venerable notion of tabula rasa so ably critiqued by evolutionary psychologists (Tooby and Cosmides 1992, Pinker 2002). According to this story, evolution gave humans large brains. The brain is empty at birth but filled with culture, including moral principles by society. Beyond providing us with the cognitive capacity to understand moral principles, we are told, biological evolution has nothing to do with morality.

According to this story, behavioral morality is the pure product of cultural evolution. This idea is famously expressed by Thomas Hobbes (1968[1651]), who writes:

The state of men without civil society (which may be called the state of nature) is nothing but a war of all against all... Where every man is enemy to every man, the life of man is solitary, poor, nasty, brutish, and short.

Some two centuries later, the influential economist Francis Ysidro Edgeworth (1881) affirmed:

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The first principle of economics is that every agent is actuated only by self-interest.

We find the same sentiment a century later in the prominent biologist Richard Dawkins (1976), who writes:

We are survival machines–robot vehicles blindly programmed to preserve the selfish molecules known as genes... Let us try to teach generosity and altruism, because we are born selfish.

The general conclusion, then, is that humans are inherently egoistic, but we can teach the young the proper way to behave, and we can enforce proper behavior by means of civilizing institutions. Morality, then, is an elaborate veneer hiding our basic self-regarding natures. The unusually provocative Michael Ghiselin (1974) writes:

No hint of genuine charity ameliorates our vision of society, once sentimentalism has been laid aside. What passes for cooperation turns out to be a mixture of opportunism and exploitation. Scratch an altruist, and watch a hypocrite bleed.

More dispassionately, the noted evolutionary biologist Richard Alexander (1987) professes:

Ethics, morality, human conduct, and the human psyche are to be understood only if societies are seen as collections of individuals seeking their own self-interest.

This paper presents a rather more sanguine appreciation of behavioral morality, based on evolutionary biology, paleontology, the rational actor model, behavioral game theory, and experimental psychology. The basic principles are:

- Behavioral morality is the product of an evolutionary dynamic extending over hundreds of thousands of years in the hominin line involving the interaction of genes and culture.

- In this dynamic, hominin societies transformed culture, and the new culture made new behaviors fitness-enhancing, transforming the hominin line itself. Thus, gene-culture coevolution: in humans, genes are the product of culture and culture is the product of genes.

- Behavioral morality, in particular, is predicated upon a set of human predispositions that evolved during our evolutionary emergence in small-scale hunter-gatherer groups.
When our ancestors developed the capacity intentionally to devise social games and play according to their culturally constituted rules, it became possible to conceive of society itself as a social game, the rules of which are determined in a new arena of social life, which we may call the public sphere.

Humans thus evolved two modes of social behavior, private persona personal preferences regulating everyday life in civil society, and their public persona regulating their behavior in the public sphere.

At the heart of our moral capacities, both as private and public persona, is the capacity to conceptualize a higher moral realm that leads us to “do the right thing,” to feel the satisfaction of doing the right thing, and to experience a degraded self when we have not done the right thing.

2 Gene-culture Coevolution

Individual fitness in humans depends on the structure of social life. For instance, if society rewards certain behaviors, then females will prefer offspring that exhibit these behaviors, and if there is a genetic element in the behaviors, they will seek mates that exhibit these behaviors as well. Thus social values entail enhanced fitness for males that carry the socially valued genes. Similarly, if social norms entail the ostracism of individuals who exhibit certain behaviors, then genes that support these behaviors are likely to be replaced in the population by genes that suppress the disfavored behaviors.

Human cognitive, affective and moral capacities are thus the product of an evolutionary dynamic involving the interaction of genes and culture. We call this dynamic gene-culture coevolution (Boyd and Richerson 1985, Cavalli-Sforza and Feldman 1982, Dunbar 1993, Richerson and Boyd 2004). This coevolutionary process has endowed us with preferences that go beyond the self-regarding concerns emphasized in traditional economic and biological theory, with a social epistemology that facilitates the sharing of intentionality across minds, and a moral sense that entails to both contributing to the social good and doing the right thing for its own sake. Gene-culture coevolution explains the salience of such other-regarding values as a taste for cooperation, fairness and retribution, the capacity to empathize, and the ability to value such character virtues as honesty, hard work, piety and loyalty.

Gene-culture coevolution is the application of sociobiology, the general theory of the social organization of biological species, to humans—a species that transmits culture in a manner that leads to its preservation across many generations.
The genome in general encodes information that is used both to construct a new organism and to endow it with instructions for transforming sensory inputs into behavioral outputs. Because learning is costly, efficient information transmission will ensure that the genome encodes those aspects of the organism’s environment that are constant, or that change only very slowly through time and space as compared with the reproduction period for the species. By contrast, environmental conditions that vary rapidly can be dealt with by providing the organism with sufficient phenotypic plasticity.

There is an intermediate case, however, that is efficiently handled neither by genetic encoding nor phenotypic plasticity. When environmental conditions are positively but imperfectly correlated across generations, each generation acquires valuable information through learning. In such cases there is a fitness benefit to information transmission through non-genetic channels. Several such transmission mechanisms have been identified (Jablonka and Lamb 1995), among which cultural transmission (Bonner 1984, Richerson and Boyd 1998) is a most flexible form. Cultural transmission takes the form of parents to children, peer to peer, and elder to younger (Cavalli-Sforza and Feldman 1981), higher to lower status (Henrich and Gil-White 2001), popularity-related (Newman et al. 2006), and even random (Shennan 1997, Skibo and Bentley 2003). The similarity of cultural and biological evolution goes back to Julian Huxley (1955), Karl Popper (1979), and William James (1880). The idea of treating culture as a form of epigenetic transmission was pioneered by Dawkins (1976), who coined the term meme in The Selfish Gene (1976). There quickly followed several major contributions to a biological approach to culture, all based on the notion that culture, like genes, could evolve through replication, mutation and selection. Culture propagates from brain to brain, mutates in replication, and is subject to selection according to its effects on the fitness of its carriers (Parsons 1964, Cavalli-Sforza and Feldman 1982).

There are strong interactions between genes and culture, ranging from basic physiology, such as the transformation of the organs of speech with the evolution of language, to sophisticated social emotions, including empathy, shame, guilt and revenge-seeking (Ihara 2011, Zajonc 1980). Because of their common informational and evolutionary character, there are strong parallels between models of genetic and cultural evolution (Mesoudi et al. 2006). Like genes, culture is transmitted from parents to offspring, and like culture, which is transmitted horizontally to unrelated individuals, so are genes in microbes and many plant species, genes are regularly transferred across lineage boundaries (Jablonka and Lamb 1995, Abbott et al. 2003, Rivera and Lake 2004).

Anthropologists reconstruct the history of social groups by analyzing homologous and analogous cultural traits, much as biologists reconstruct the evolution of species by the analysis of shared characters and homologous DNA (Mace and
Indeed, the same computer programs developed by biological systematists are used by cultural anthropologists (Holden 2002, Holden and Mace 2003). In addition, archeologists who study cultural evolution have a *modus operandi* similar to palaeobiologists who study genetic evolution (Mesoudi et al. 2006). Both attempt to reconstruct lineages of artifacts and their carriers. Like palaeobiologists, archaeologists assume that when analogy can be ruled out, similarity implies causal connection by inheritance (O’Brien and Lyman 2000). Like biogeographers’ study of the spatial distribution of organisms (Brown and Lomolino 1998), behavioral ecologists study the interaction of ecological, historical and geographical factors that determine distribution of cultural forms across space and time (Winterhalder and Smith 1992).

Perhaps the most common criticism of the analogy between genetic and cultural evolution is that the gene is a well-defined, discrete, independently reproducing and mutating entity, whereas the boundaries of the unit of culture are ill-defined and overlapping. However, this view of the gene is outdated. We now know that overlapping, nested and movable genes have some of the fluidity of cultural units, whereas quite often the boundaries of a cultural unit (a belief, icon, word, technique, stylistic convention) are quite delimited and specific. Similarly, alternative splicing, nuclear and messenger RNA editing, cellular protein modification and genomic imprinting, which are quite common, undermine the standard view of the insular gene coding for a single protein, and support the notion of genes having variable boundaries and strongly context-dependent effects. Moreover, natural selection requires heritable variation and selection, but does not require discretely transmitted units.

Dawkins (1982) added a second fundamental mechanism of epigenetic information transmission, noting that organisms can directly transmit environmental artifacts to the next generation, in the form of such constructs as beaver dams, bee hives and even social practices (e.g. mating rituals and hunting strategies). (Odling-Snee et al. 2003, Gintis 2014).

An excellent example of gene-environment coevolution is the honeybee, in which the origin of its eusociality probably lay in a high degree of relatedness, but which persists in modern species despite the fact that relatedness in the hive is generally quite low, due to multiple queen matings, multiple queens, queen deaths and the like (Gadagkar 1991, Seeley 1997, Wilson and Hölldobler 2005). The social structure of the hive, a classic example of niche construction, is transmitted genetically across generations, and the honeybee genome is an adaptation to the social structure of the hive laid down in the distant past.

Gene-culture coevolution in humans is a special case of gene-environment coevolution in which the environment is culturally constituted and transmitted (Feldman and Zhivotovsky 1992). The key to the success of our species in the framework
of the hunter-gatherer social structure in which we evolved is the capacity of genealogically unrelated individuals to cooperate in large egalitarian groups in hunting, territorial acquisition, and defense (Boehm 1999, Richerson and Boyd 2004). While some contemporary biological and economic theorists have attempted to show that such cooperation can be supported by self-regarding rational agents (Trivers 1971, Alexander 1987, Fudenberg et al. 1994), the conditions under which their models work are implausible even for small groups (Boyd and Richerson 1988, Gintis 2009, Bowles and Gintis 2011). Rather, the social environment of early humans was conducive to the development of prosocial traits, such as empathy, shame, pride, embarrassment and reciprocity, without which social cooperation would be impossible (Sterelny 2011).

Neuroscientific studies exhibit clearly the genetic basis for moral behavior. Brain regions involved in moral judgments and behavior include the prefrontal cortex, the orbital frontal cortex and the superior temporal sulcus (Moll et al. 2005). These brain structures are virtually unique to or most highly developed in humans and are doubtless evolutionary adaptations (Schulkin 2000). The evolution of the human prefrontal cortex is closely tied to the emergence of human morality (Allman et al. 2002). Patients with focal damage to one or more of these areas exhibit a variety of antisocial behaviors, including the absence of embarrassment, pride and regret (Beer et al. 2003, Camille 2004), as well as sociopathic behavior (Miller et al. 1997). There is a probable genetic predisposition underlying sociopathy, and sociopaths comprise 3–4% of the male population, but they account for between 33 and 80 per cent of the population of chronic criminal offenders in the United States (Mednick et al. 1977). It is clear from this body of empirical information that culture is directly encoded into the human brain with symbolic representations in the form of cultural artifacts. This, of course, is the central claim of gene-culture coevolutionary theory.

2.1 Culture to Genes: The Physiology of Communication

The evolution of the physiology of speech and facial communication is a dramatic example of gene-culture coevolution. The increased social importance of communication in human society rewarded genetic changes that facilitate speech. Regions in the motor cortex expanded in early humans to facilitate speech production. Concurrently, nerves and muscles to the mouth, larynx and tongue became more numerous to handle the complexities of speech (Jurmain et al. 1997). Parts of the cerebral cortex, Broca’s and Wernicke’s areas, which do not exist or are relatively small in other primates, are large in humans and permit grammatical speech and comprehension (Belin et al. 2000, Binder et al. 1997).
Modern humans have a larynx low in the throat, a position that allows the throat to serve as a resonating chamber capable of a great number of sounds (Relethford 2007). The first hominids that have skeletal structures supporting this laryngeal placement are the Homo heidelbergensis, who lived from 800,000 to 100,000 years ago. In addition, the production of consonants requires a short oral cavity, whereas our nearest primate relatives have much too long an oral cavity for this purpose. The position of the hyoid bone, which is a point of attachment for a tongue muscle, developed in Homo sapiens in a manner permitting highly precise and flexible tongue movements.

Another indication that the tongue has evolved in hominids to facilitate speech is the size of the hypoglossal canal, an aperture that permits the hypoglossal nerve to reach the tongue muscles. This aperture is much larger in Neanderthals and humans than in early hominids and non-human primates (Dunbar 2005). Human facial nerves and musculature have also evolved to facilitate communication. This musculature is present in all vertebrates, but except in mammals it serves feeding and respiratory functions alone (Burrows 2008). In mammals, this mimetic musculature attaches to the skin of the face, thus permitting the facial communication of such emotions as fear, surprise, disgust and anger. In most mammals, however, a few wide sheetlike muscles are involved, rendering fine information differentiation impossible, whereas in primates, this musculature divides into many independent muscles with distinct points of attachment to the epidermis, thus permitting higher bandwidth facial communication. Humans have the most highly developed facial musculature by far of any primate species, with a degree of involvement of lips and eyes that is not present in any other species.

In short, humans have evolved a highly specialized and very costly array of physiological characteristics that both presuppose and facilitate sophisticated vocal and visual communication, whereas communication in other primates, lacking as they are in cumulative culture, goes little beyond simple calling and gesturing capacities involving adoption of communicative physiology. This example is quite a dramatic and concrete illustration of the intimate interaction of genes and culture in the evolution of our species.

3 The Rationality of Morality

Behavioral morality involves making personally costly choices that promote ethical goals. People not only balance self-regarding against moral concerns, but also face conflicting moral principles in making choices. We therefore model choice behavior using the rational actor model, according to which individuals have a preference function representing their goals, they face constraints that limit the mix
of goals available to them, and they have beliefs concerning how their actions affect the probability of attaining their goals. This concept of rationality is extremely skeletal, strongly favoring the consistency principles of formal rationality with little regard for the actors' substantive rationality; i.e., the extent to which behavior is attuned to achieving any particular standard measure, such as fitness, well-being, or happiness. Preferences, for instance, may include such self-regarding goals as material wealth and leisure, such other-regarding goals fairness, consideration for the welfare of others, and such character virtues as honesty, loyalty, trustworthiness, courage, and considerateness that have intrinsic value independent of their effects. Moreover, we impose no plausibility constraints on beliefs.

The rational actor model assumes but does not explain the pattern of individual preferences. Understanding preferences requires forays into the psychology of goal-directed, moral behavior (Haidt 2012), social evolutionary theory (Tooby and Cosmides 1992), and problem-solving heuristics (Gigerenzer and Todd 1999).

The most important single contribution to the theory of formal rational choice was that of Leonard Savage (1954), who showed that a small set of plausible choice axioms (the Savage axioms) implies that a rational actor can be modeled as maximizing an objective function subject to the constraints he faces, where his beliefs take the form of a subjective prior specifying the agent’s judgment as to the probabilistic effects of his actions on the attainment of his goals. This objective function is often called a utility function, although the term is misleading because the objective function in the rational actor model need have no utilitarian content. The most important of the Savage axioms is that the agent’s preferences are transitive in the sense that if he prefers A to B and he also prefers B to C, then he must also prefer A to C. The remaining assumptions are rather technical and not relevant for our purposes (Savage 1954, Gintis 2009, Gintis and Helbing forthcoming).

The Savage axioms do not suggest that an agent chooses what is in his best interest or what gives him pleasure. Nor do the axioms suggest that the actor is selfish, calculating, or amoral. Finally, the Savage axioms do not suggest that the rational actor is trying to maximize utility or anything else. The maximization formulation of rational choice behavior is simply an analytical convenience, akin to the least action principle in classical mechanics, or predicting the behavior of an expert billiards player by solving a set of differential equations of which the expert has not the least awareness. The theory flowing from the Savage axioms is a powerful tool that is valid whatever the nature of human goals and motivations, provided they involve consistent choices.
4 A Typology of Rational Action

Human actors exhibit three types of motives in their daily lives: self-regarding, other-regarding, and universalist. Self-regarding motives include seeking wealth, consumption, leisure, social reputation, status, esteem, and other markers of personal advantage. Other-regarding motives include reciprocity, fairness, and concern for furthering the well-being of others. Universalist motives are those that are followed for their own sake rather than directly for their effects. Among these universalist goals, which we term character virtues, are honesty, loyalty, courage, trustworthiness, and considerateness. Of course, such universalist goals normally have consequences for those with whom one interacts, and for society as a whole. But one undertakes universalist actions for their own sake, beyond any consideration of their effects. I will give one example of other-regarding behavior and another of universalist behavior, as revealed by laboratory experiments using behavioral game theory.

4.1 Positive Reciprocity: The Trust Game

Positive reciprocity takes the form of individual responding to an act of kindness by returning the kindness. Positive reciprocity can be self-regarding because returning favors help create and sustain a mutually rewarding relationship. Robert Trivers (1971) called such tit-for-tat behavior reciprocal altruism, but there is in fact no altruism at all involved, since a purely selfish individual will engage in this form of positive reciprocity. However, humans also exhibit positive reciprocity when there is no possibility of future gain from the costly act of returning a kindness. We call this other-regarding behavior positive reciprocity, or altruistic cooperation.

For example, consider the trust game, first studied by Berg et al. (1995). In this game, carried out in a experimental laboratory, subjects are each given an endowment, say $10. Subjects are then randomly paired, and one subject in each pair, whom we will call the Proposer, is told he can transfer any number of dollars, from zero to ten, to his anonymous partner, whom we will call the Responent, and the Proposer can keep the remainder. The amount transferred will be tripled by the experimenter and given to the Responent, who can then give any number of dollars back to the Proposer (this amount is not tripled). A Proposer who transfers a lot is called trusting, and a Responent who returns a lot to the Proposer is called trustworthy. This interaction occurs only one time, and the Proposer and the Responent never learn each other’s identity. Trustworthiness is thus a pure act of other-regarding positive reciprocity.

Berg et al. (1995) found that on average, the Proposer transferred $5.16 of the $10.00 to the Responent, and on average, the Responent transferred back $4.66 the
Proposer. Furthermore, when the experimenters revealed this result to the subjects and had them play the game a second time, on average $5.36 was transferred from the Proposer to the Responder, and $6.46 was transferred back from the Responder to the Proposer. In both sets of games there was a great deal of variability, some the Proposers transferring everything, some nothing, and some Respondents more than fully repaying their Proposers and others returning nothing.

4.2 Negative Reciprocity: The Ultimatum Game

Negative reciprocity occurs when an individual responds to an unkind act by retaliating with another unkind act. Negative reciprocity can be self-regarding because retaliation may induce the other person to behave more kindly in the future, and more generally one may thereby enhance one’s reputation as someone not to be trifled with. There is no moral element in this sort of negative reciprocity, since a purely selfish individual may retaliate to enhance his reputation and thereby deter future unkind acts. However, humans also exhibit negative reciprocity when there is no possibility of future interaction with the offender. We call this other-regarding negative reciprocity *altruistic punishment*.

The simplest game exhibiting altruistic punishment is the Ultimatum Game (Güth et al. 1982). Under conditions of anonymity, two subjects, whom we will call Alice and Bob, are shown a sum of money, say $10. Alice, called the Proposer, is instructed to offer any number of dollars, from $1 to $10, to Bob, who is called the Responder. Alice can make only one offer and Bob can either accept or reject this offer. If Bob accepts the offer, the money is split according to Alice’s offer. If Bob rejects the offer, both players receive nothing. Alice and Bob, who are unknown to each other, do not interact again.

If Bob is self-regarding, he will accept anything he is offered. If Alice believes Bob is self-regarding, she will offer him the minimum amount ($1) and Bob will accept. However, when actually played, this self-regarding outcome is almost never observed or even approximated. In fact, under varying conditions and with varying amounts of money, Proposers routinely offer Responders very substantial amounts (50% of the total generally being the modal offer) and Responders frequently reject offers below 30% (Güth and Tietz 1990, Camerer and Thaler 1995).

Are these results culturally dependent? Do they have a strong genetic component or do all successful cultures transmit similar values of reciprocity to individuals? Roth et al. (1991) conducted the Ultimatum Game in four different countries (United States, the former Yugoslavia, Japan, and Israel) and found that while the level of offers differed a small but significant amount in different countries, the probability of an offer being rejected did not. This indicates that both Proposers
and Responders share the same notion of what is considered fair in that society and that Proposers adjust their offers to reflect this common notion. When a much greater degree of cultural diversity is studied, however, large differences in behavior are found, reflecting different standards of what it means to be fair in different types of societies (Henrich et al. 2004).

Behavior in the Ultimatum Game conforms to the altruistic punishment model. Responders reject offers under 40% to hurt an unfair Proposer. Proposers offer 50% because they are altruistic cooperators, or 40% because they fear rejection. To support this interpretation, we note that if the offers in an Ultimatum Game are generated by a computer rather than by the Proposer, and if Responders know this, low offers are rarely rejected (Blount 1995). This suggests that players are motivated by reciprocity, reacting to a violation of behavioral norms (Greenberg and Frisch 1972). Moreover, in a variant of the game in which a Responder rejection leads to the Responder getting nothing but allows the Proposer to keep the share he suggested for himself, Responders never reject offers, and proposers make considerably smaller (but still positive) offers (Bolton and Zwick 1995). As a final indication that altruistic punishment motives are operative in this game, after the game is over, when asked why they offered more than the lowest possible amount, Proposers commonly said that they were afraid that Responders will consider low offers unfair and reject them. When Responders rejected offers, they usually claimed they want to punish unfair behavior. In all of the above experiments a significant fraction of subjects (about a quarter, typically) conformed to purely self-regarding preferences.

### 4.3 A Universalist Character Virtue: Honesty

Certain moral behaviors are universalist in the sense that one performs them, at least in part, because it is virtuous to do so, apart from any effects they have on oneself, others, or society in general. For instance, one can be honest in dealing with another agent without caring at all about the effect on the other agent, or even caring about the impact of honest behavior on society at large. Similarly, one can be courageous in battle because it is the right thing to do, independent from the effect of one’s actions on winning or losing the battle.

A particularly clear example of the value of honesty is reported by Gneezy (2005), who studied 450 undergraduate participants paired off to play three games of the following form, all payoffs to which are of the form \((a, b)\) where player 1 (Alice) receives \(a\) and Player 2 (Bob) receives \(b\). In all games, Alice was shown two pairs of payoffs, \(A: (x, y)\) and \(B: (z, w)\) where \(x, y, z,\) and \(w\) are amounts of money with \(x < z\) and \(y > w\), so in all cases, \(B\) is better for Bob and \(A\) is
better for Alice. Alice could then say to Bob, who could not see the amounts of
to Bob, either “Option A will earn you more money than option B,” or “Option B will earn you more money than option A.” The first game was A:(5,6) vs. B:(6,5)
so Alice could gain 1 by lying and being believed, while imposing a cost of 1 on Bob. The second game was A:(5,15) vs. B:(6,5) so Alice could gain 10 by lying and being believed, while still imposing a cost of 1 on Bob. The third game was A:(5,15) versus B:(15,5), so Alice could gain 10 by lying and being believed, while imposing a cost of 10 on Bob.

Before starting play, the experimenter asked each Alice whether she expected her advice to be followed, inducing honest responses by promising to reward her if her guesses were correct. He found that 82% of Alices expected their advice to be followed (the actual result was that 78% of Bobs followed their Alice’s advice). It follows that if Alices were self-regarding, they would always lie and recommend B to their Bob.

The experimenters found that, in game two, where lying was very costly to Bob and the gain to lying for Alice was small, only 17% of subjects lied. In game one, where the cost of lying to Bob was only one but the gain to Alice was the same as in game two, 36% lied. In other words, subjects were loathe to lie, but considerably more so when it was costly to their partner. In game three, where the gain from lying was large for Alice, and equal to the loss to Bob, fully 52% lied. This shows that many subjects are willing to sacrifice material gain to avoid lying in a one-shot, anonymous interaction, their willingness to lie increasing with an increased cost of truth-telling to themselves, and decreasing with an increase in their partner’s cost of begin deceived. Similar results were found by Boles et al. (2000) and Charness and Dufwenberg (2006). Gunnthorsdottir et al. (2002) and Burks et al. (2003) have shown that a social-psychological measure of “Machiavellianism” predicts which subjects are likely to be trustworthy and trusting.

5 The Public Sphere

The social life of most species, including mating practices, symbolic communication, and power relations, is inscribed in its core genome, and expressed in stereotypical form by its members (Gintis 2014). Homo sapiens is unique in adapting its social life in fundamental and deep-rooted ways to environmental challenges and opportunities (Richerson and Boyd 2004). This flexibility is based on two aspects of our mental powers. The first is our ability to devise new rules of the game in social life, and to base our social interaction on these new rules. This capacity, absent in other species, makes us Homo Ludens: Man the game player. This capacity is possessed even by very young children who invent, understand, and play games
for fun. In adult life, this same capacity is exercised when people come together to erect, protect, and transform the social rules that govern their daily lives. Broadly speaking, we can define the public sphere as the arena in which society-wide rules of the game are considered, and politics as the cooperative, conflictual, and competitive behaviors through which rules are established and individuals are assigned to particular public positions.

Humans evolved in hunter-gather societies consisting of a dozen families or so (Kelly 1995), in which political life was an intimate part of daily life, involving the sorts of self-regarding, other-regarding, and universalistic motivations described above. In particular, political activity was strongly consequentialist: a single individual could expect to make a difference to the outcome of a deliberation, a conflict, or a collaboration, so that our political morality developed intimately entwined with material interests and everyday consequentialist moral sentiments (Boehm 1999, Gintis et al. in press).

As we move from small-scale hunter-gatherer societies to modern mass societies with millions of members, the public sphere passes from being intimately embedded in daily life to being a largely detached institutional arena, governed by complex institutions controlled by a small set of individuals, and over which most members have at best formal influence through the ballot box, and at worst no formal influence whatever. Political activity in modern societies is thus predominately non-consequentialist, meaning that individuals do not base their choices on the effect of their actions on political outcomes. Except for a small minority of individuals contesting for personal power, the political choices of a single citizen affects public sphere outcomes with a probability very close to zero—sufficiently close that these choices cannot not be attributed to consequentialist motives, whether self-regarding, other-regarding, or universalist.

In large elections, the rational consequentialist agent will not vote because the costs of voting are positive and significant, but the probability that one vote will alter the outcome of the election is vanishingly small, and adding a single vote to the total of a winning candidate enhances the winner’s political efficacy at best an infinitesimal amount (Downs 1957, Riker and Ordeshook 1968). Thus the personal consequentialist gain from voting is too small to motivate behavior even for a committed other-regarding or universalist altruist (Hamlin and Jennings 2011). For similar reasons, if one chooses to vote, there is no plausible reason to vote on the basis of the impact of the outcome of the election on one’s personal material gains, or on the basis of the gains to the demographic and social groups to which one belongs, or even on the basis of consequentialist universal values. One vote simply makes no difference. It follows also that the voter, if rational and consequentialist, and incapable of personally influencing the opinions of more than a few others, will not bother to form opinions on political issues, because these opinions
cannot affect the outcome of elections. Yet people do vote, and many do expend time and energy in forming political opinions. Although voters do appear to behave strategically (Fedderson and Sandroni 2006), their behavior does not conform to the rational consequentialist model (Edlin et al. 2007).

It also follows that rational consequentialist individuals will not participate in the sort of collective actions that are responsible for the growth in the world of representative and democratic governance, the respect for civil liberties, the rights of minorities and gender equality in public life, and the like. In the rational consequentialist model, only small groups aspiring for social dominance will act politically. Yet modern egalitarian political institutions are the result of such collective actions (Bowles and Gintis 1986, Giugni et al. 1998). This behavior cannot be explained by a rational consequentialist model.

Except for professional politicians and socially influential individuals, electoral politics is a vast morality play to which our consequentialist models of the rational actor are a poor fit. Mancur Olson argued as much in his classic, The Logic of Collective Action (1965), but behavioral scientists have yet to come fully to grips with its iron-clad logic (Downs 1957, Hamlin and Jennings 2011).

Defenders of the rational consequentialist model (there are very few) might respond that voters believe their votes make a difference, however poorly this belief might survive logical scrutiny. Indeed, when asked why they vote, voters’ commonly respond that they are trying to help get one or another party elected to office. When apprised of the illogical character of that response, given that a single vote in a large election cannot make a difference, they commonly reply that there are in fact close national elections, where the balance is tipped in one direction or another by only a few hundred votes. When reminded that one vote will not affect even such close elections, the common reply is that “Well, if everyone thought like that, then no one would vote and we could not have a democracy.”

Politically active and informed citizens appear to operate on the principle that voting and participating in collective actions are highly valued non-consequentialist behaviors. This idea is difficult for people to articulate because the consequentialist vs. non-consequentialist distinction is not part of either common parlance or the specialized lexicon of political theory. However, most voters agree with statements like “my single vote won’t make a difference, but if all concerned citizens vote our common concerns, we can make a difference.” Of course it does not logically follow that one should vote according to standard decision theory because if “my single vote won’t make a difference,” then I still have no consequentialist reason for voting.

However, humans appear to follow a non-consequentialist logic that may be summarized as rule-consequentialism: in public life, choose a rule that like-minded people might plausibly choose, and if followed by all of us, will lead to the most de-
sirable outcome (Harsanyi 1977, Hooker 2011, Roemer 2010). Rule-consequentialism explains why people are perfectly reasonable in assenting to such assertion as “I am helping my candidate win by voting” and “I am helping promote democracy by demonstrating against the dictator” are literally correct. Because rule-consequentialism is so ingrained in our public persona, people untrained in traditional rational decision theory simply cannot understand the argument that it is irrational to vote or to participate in collective actions, even when they can be persuaded that their actions are non-consequential.

Rule-consequentialism can also explain many stylized facts of voter behavior. First, when the cost of voting increases, fewer people vote. The rule here is something like “My unusual personal situation means voting would be very costly to me today. I would not expect anyone in my position to vote, so I am comfortable with not voting.” Second, it explains why voter turnout is higher when the issues to be decided have greater social impact. Third, it explains why turnout is higher when the election is expected to be close. Finally, it explains why, in a two-party election, turnout is likely to be higher among voters for the side that is not expected to win. Indeed, it is reasonable to speculate that rule-consequentialism leads voters to act in very large elections in much the same way they would in very small elections, although in very small elections consequentialist issues (e.g., self-interested) may trump the non-consequentialist rule.

We conclude that the individual immersed in consequentialist everyday life expresses his private persona, while his behavior in the public sphere reveals his public persona. Individuals acting in the public sphere, are, then a different sort of animal, one which Aristotle called zoon politikon in his Nicomachean Ethics.

6 Private and Public Persona

The concept of a non-consequentialist public persona suggests a two by three categorization of human motivations, as presented in Figure 1. In this figure, the three columns represent three modes of social interaction. The personal mode is purely self-regarding, while the social mode represents the agent as embedded in a network of significant social relations, and the universal represents the individual’s realm of recognized supra-situational moral obligations. The two rows represent the agent’s private persona of consequentialist social relations in civil society, and the agent’s public persona of non-consequentialist political relationships in the public sphere.

Homo Economicus is the venerable rational selfish maximizer of traditional economic theory, Homo Socialis is the other-regarding agent who cares about fairness, reciprocity, and the well-being of others, and Homo Moralis is the Aris-
totelian bearer of non-consequentialist character virtues. The new types of public persona are *Homo Autisticus* who behaves politically just as *Homo Economicus* does privately, while *Homo Parochialis* votes and engages in collective action on behalf of the narrow interests of the demographic, ethnic and/or social status groups with which he identifies. Finally, *Homo Universalis* acts politically to achieve what he considers the best state for the larger society, for instance, reflecting John Rawls’ (1971) *veil of ignorance*, John Harsanyi’s (1977) *criterion of universality*, or John Roemer’s (2010) *Kantian equilibrium*.

Probably *Homo Autisticus* does not exist because a self-regarding agent will never do anything except for its consequences, and the concept of rule-consequentialism is difficult to comprehend when one is the only “like-minded” person. Interestingly, the individual whose private persona is social is generally considered altruistic, whereas the individual whose public persona is social is often considered selfish, acting in a partisan manner on behalf of the narrow interests of the social networks to which he belongs. Of course *Homo Parochialis* is altruistic towards these social networks.

7 The Evolutionary Emergence of Private Morality

By *cooperation* we mean engaging with others in a mutually beneficial activity. Cooperative behavior may confer net benefits on the individual cooperator, and thus can be motivated entirely by self-interest. In this case, cooperation is a form of *mutualism*. Cooperation may also be a net cost to the individual but the benefits may accrue to a close relative. We call this *kin altruism*. Cooperation can additionally take the form of one individual’s costly contribution to the welfare of another individual being reliably reciprocated at a future date. This is often called *reciprocal altruism* (Trivers 1971), although it is really just *tit-for-tat* mutualism. However, important forms of cooperation impose net costs upon individuals, the beneficiaries many not be close kin, and the benefit to others may not be expected to be repaid in the future. This cooperative behavior is true altruism.

The evolution of mutualistic cooperation and kin altruism is easily explained.
Cooperation among close family members evolves by natural selection because the benefits of cooperative actions are conferred on the close genetic relatives of the cooperator, thereby helping to proliferate genes associated with the cooperative behavior. Kin altruism and mutualism explain many forms of human cooperation, particularly those occurring in families or in frequently repeated two-person interactions. But these models fail to explain two facts about human cooperation: that it takes place in groups far larger than the immediate family, and that both in real life and in laboratory experiments, it occurs in interactions that are unlikely to be repeated, and where it is impossible to obtain reputational gains from cooperating. These forms of behavior are regulated by moral sentiments.

The most parsimonious proximal explanation of altruistic cooperation, one that is supported by extensive experimental and everyday-life evidence, is that people gain pleasure from cooperating and feel morally obligated to cooperate with like-minded people. People also enjoy punishing those who exploit the cooperation of others. Free-riders frequently feel guilty, and if they are sanctioned by others, they may feel ashamed. We term these feelings social preferences. Social preferences include a concern, positive or negative, for the well being of others, as well as a desire to uphold ethical norms.

7.1 The Roots of Social Preferences

Why are the social preferences that sustain altruistic cooperation in daily life so common? Early human environments are part of the answer. Our Late Pleistocene ancestors inhabited the large-mammal-rich African savannah and other environments in which cooperation in acquiring and sharing food yielded substantial benefits at relatively low cost. The slow human life-history with prolonged periods of dependency of the young also made the cooperation of non-kin in child rearing and provisioning beneficial. As a result, members of groups that sustained cooperative strategies for provisioning, child-rearing, sanctioning non-cooperators, defending against hostile neighbors, and truthfully sharing information had significant advantages over members of non-cooperative groups.

There are several reasons why these altruistic social preferences supporting cooperation outcompeted amoral self-interest. First, human groups devised ways to protect their altruistic members from exploitation by the self-regarding. Prominent among these is the collective punishment of miscreants (Boyd et al. 2010), including the public-spirited shunning, ostracism, and even execution of free-riders and others who violate cooperative norms.

Second, humans adopted elaborate systems of socialization that led individuals to internalize the norms that induce cooperation, so that contributing to common
projects and punishing defectors became objectives in their own right rather than constraints on behavior. Together, the internalization of norms and the protection of the altruists from exploitation served to offset, at least partially, the competitive handicaps born by those who were motivated to bear personal costs to benefit others.

Third, between-group competition for resources and survival was and remains a decisive force in human evolutionary dynamics. Groups with many cooperative members tended to survive these challenges and to encroach upon the territory of the less cooperative groups, thereby both gaining reproductive advantages and proliferating cooperative behaviors through cultural transmission. The extraordinarily high stakes of intergroup competition and the contribution of altruistic cooperators to success in these contests meant that sacrifice on behalf of others, extending beyond the immediate family and even to virtual strangers, could proliferate (Choi and Bowles 2007, Bowles 2009).

This is part of the reason why humans became extraordinarily group-minded, favoring cooperation with insiders and often expressing hostility toward outsiders. Boundary-maintenance supported within-group cooperation and exchange by limiting group size and within-group linguistic, normative and other forms of heterogeneity. Insider favoritism also sustained the between-group conflicts and differences in behavior that made group competition a powerful evolutionary force.

In short, we became a cooperative species because cooperation was highly beneficial to the members of groups that practiced it, and we were able to construct social institutions that minimized the disadvantages of those with social preferences in competition with self-regarding fellow group members, while heightening the group-level advantages associated with the high levels of cooperation that these social preferences allowed. These institutions proliferated because the groups that adopted them secured high levels of within-group cooperation, which in turn favored the groups’ survival as a biological and cultural entity in the face of environmental, military and other challenges.

8 The Evolutionary Emergence of the Public Persona

Non-human species, even if highly social, do not engage in activities that structure the social rules that regulate their lives. Therefore there is no politics and no public sphere in these species, and hence its members have no public persona. How, then, might a public persona have arisen in the hominin line leading up to Homo sapiens?

In a related paper, Carel van Schaik, Christopher Boehm, and I (Gintis et al. in press) supply a answer grounded in the information available to us from a variety
of fields, including paleontology, primatology, the anthropology of contemporary hunter-gatherer groups, animal behavior theory, and genetics. We propose that the emergence of bipedalism, cooperative breeding, and lethal weapons (stones and wooden spears) in the hominin line, together with favorable climate change, made the collaborative hunting and scavenging of large game fitness enhancing. Lethal weapons are the most unique of these innovations, for other predators, such as lions, tigers and other big cats, wolves, foxes and other canines, use only their natural weapons—sharp claws and teeth, powerful jaws and great speed—in hunting, while none of these endowments was available to early hominins. Lethal hunting weapons, moreover, transformed human sociopolitical life because they could be applied to humans just as easily as to other animals.

The combination of the need for collaboration and the availability of lethal weapons in early hominin society undermined the social dominance hierarchy characteristic of primate and earlier hominin groups, which was based on pure physical prowess. The successful sociopolitical structure that ultimately replaced the ancestral social dominance hierarchy was an egalitarian political system in which lethal weapons made possible group control of leaders, group success depended on the ability of leaders to persuade and motivate, and of followers to contribute to a consensual decision process. The heightened social value of non-authoritarian leadership entailed enhanced biological fitness for such leadership traits as linguistic facility, ability to form and influence coalitions, and indeed for hypercognition in general.

This egalitarian political system persisted until cultural changes in the Holocene fostered the accumulation of material wealth, through which it became possible once again to sustain a social dominance hierarchy with strong authoritarian leaders.

9 Conclusion

This paper has provided evidence for a model of human behavior based on the rational actor model, in which individuals have both private and public persona, and their preferences range over personal, social, and universal modes of our private persona and in most of our activities in the public sphere. Morality in this model is defined in behavioral terms: moral choices are those made in social and universalist modes. The public sphere in this model is an arena where preferences and actions are primarily non-consequentialist. The other-regarding preferences of Homo Socialis and the character virtues of Homo Vertus are underpinnings of civil society, while Homo Parochialis and Homo Universalis make possible the varieties of political life characteristic of our species.
References


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