

Tribal Social Instincts and the Cultural Evolution of Institutions to Solve Collective Action Problems

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Human social life is uniquely complex and diverse. Much of that complexity and diversity arises from culturally transmitted ideas, values and skills that underpin the operation of social norms and institutions that structure our social life. Considerable theoretical and empirical work has been devoted to the role of cultural evolutionary processes in the evolution of social norms and institutions. The most persistent controversy has been over the role of cultural group selection and gene-culture coevolution in early human populations during Pleistocene. We argue that cultural group selection and related cultural evolutionary processes had an important role in shaping the innate components of our social psychology. By the Upper Paleolithic humans seem to have lived in societies structured by institutions, as do modern populations living in small-scale societies. The most ambitious attempts to test these ideas have been the use of experimental games in field settings to document human similarities and differences on theoretically interesting dimensions. These studies have documented a huge range of behavior across populations, although no societies so far examined follow the expectations of selfish rationality. These data are at least consistent with operation of cultural group selection and gene-culture coevolution operating in the deep tribal past and with the contemporary importance of cultural evolution in the evolution of institutions and institutional diversity.

Introduction

This paper summarizes research pursuing an evolutionary approach to norms, institutions, and collective action. An emerging view is that institutions arise as the joint products of our evolved psychology, which includes products of culture-gene coevolution (our tribal instincts), and ongoing cultural evolution. Cultural evolution, founded on our sophisticated evolved capacities for social learning, spontaneously gives rise to social norms and institutions as individuals interact and learn. These institutions may or may not address

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collective action problems, though they are capable of sustaining individually costly behavior in a variety of ways. Competition among institutions, and institutional forms, has over the long span of human history, favored the spread of increasingly group-beneficial institutions. Institutions involving costly punishment, for example, seem to be more elaborate and more important in larger human groups, suggesting much relatively recent cultural evolution (< 10,000 years) (Henrich et al. 2010).

This evolutionary approach can address a number of important challenges regarding collective action and large-scale human cooperation (Chudek and Henrich 2010; Henrich and Henrich 2007). These are

- 1) Why is the scale and intensity of human cooperation (and conflict) so different from other vertebrates?
- 2) Why does the scale vary so much among human societies, with some societies entirely lacking collective action beyond the extended family while others organize millions in modern nation-states?
- 3) Why are the solutions to dilemmas of cooperation reached by different societies so diverse?
- 4) Why do societies sometimes possess norms and institutions that are maladaptive and costly to individuals and groups?

We return to these four challenges at the close of our paper.

From a policy perspective, the theoretical tools that cultural evolutionary theory has begun to develop constitute a conceptual grammar for decomposing institutions on the ground and understanding how they work. This means that addressing specific problems in particular places demands applying this conceptual grammar principally through quantitative ethnography. There is just no quick and dirty substitute for observing how local institutions work (or fail), and understanding the local cultural psychology that underpins how they work. Once local institutions are understood, we think that work on our evolved psychology, including our coevolutionary tribal psychology and aspects of our capacities for cultural learning, provide a menu of tactics for calibrating, adapting, and augmenting local institutions. However, only in-depth knowledge of how specific institutions work can help avoid good-hearted efforts that inadvertently damage the norms and institutions that permit collective action (Frey and Jegen 2001).

Let's first provide our working definitions of *norms* and *institutions*. *Norms* are mental representations stored in individual brains that got there through some form of learning, broadly defined (i.e., they are not innate). Conceptually, depending on your preference and disciplinary background, *norms* could be composed of a combination of preferences and beliefs, mental

models (or scripts and schema) and motivations, or decision rules and expectations. In general, these all aim to include (1) what people believe others will do, and (2) what they think they and others ought to do, as well as (3) varying degrees (including zero) of internalized motivations to meet those expectations, and to see others meet those expectations. We argue that humans possess an evolved mechanism that facilitates acquiring local norms (Chudek and Henrich 2010).

Institutions are emergent phenomena that arise at the population- or group-level from the individuals' interactions, decisions, and learning. They are first and foremost self-reinforcing, dynamically stable equilibria that arise as individuals' norms converge and complement each other over time (Aoki 2001; Greif 2006). Typically, the participating individuals have incomplete knowledge of the institutions they participate in. For example, if the institution involves a division of labor, participating specialists in one element of the division may only know a subset of the norms of another element, the subset needed to properly operate the linkage between the two kinds of specialists. They may know little or nothing of the norms involving members of the other specialty (Barth 1965; Henrich and Boyd 2008). Another example that we have worked on is the modern institution of monogamous marriage, which provides a wide range of group-benefits to societies under certain socioeconomic conditions (Henrich et al. 2012). Few members of these societies, however, understand how or why this institution works the way it does, and do not prefer these institutions *because* of their societal-level benefits.

The Evolution of Norms and Institutions

As an empirical phenomenon, anthropologists, sociologists, and others from across the social sciences have long noted the existence of both social norms and institutions, often evoking each to explain behavioral similarities within groups, or to differentiate groups and societies. However, despite the wide usage and seemingly broad empirical importance of these concepts (Bendor and Swistak 2001), they have long lacked sufficient micro-level foundations to be taken seriously by researchers in the economic and evolutionary sciences. Without at least plausible answers to key theoretical questions regarding how social norms and institutions emerge, why individuals might adopt norms that violate their self-interest (and what 'adopt' means), how individuals' decisions interact with institutions, how institutions spread across groups, and how and why norms and institutions have changed over human history, neither concept can be fully incorporated into either economic or evolutionary frameworks. In recent decades, however, approaches arising from both evolutionary biology and economics are converging on a 'ground-up' or 'first principles' explanation of social norms and institutions (Richerson and Boyd 2005; Turchin 2009,

2010). There are now plausible theoretical answers to the above questions, and in some cases there is an overabundance of plausible answers.

The Genetic Evolution Capacities for Cultural Learning

The first step in approaching these questions from an evolutionary perspective involves deploying logic of natural selection, aided by formal evolutionary modeling, to hypothesize what kinds of learning strategies or heuristics should individuals—be they toddlers or song birds—use to adapt to uncertain, novel and/or changing environments, including environments involving social interactions (Boyd and Richerson 1985). In such environments, information about the costs and benefits of alternative behaviors is costly, or sometimes impossible to acquire. In such environments social learning strategies, which include heuristics like ‘copy the most successful’ or ‘copy the majority,’ can outcompete learning strategies that rely solely on the direct evaluation of perceived costs and benefits (Laland 2004). This approach, however, does not suggest that people don’t evaluate costs and benefits directly (of course, they do), but instead it suggests that straight cost-benefit evaluations of alternatives is only one component in a suite of strategies that permit individuals to adapt to diverse, changing, or low-information environments. Evolutionary hypotheses about cultural learning have been subdivided into those that rely on the ‘context’ in which a representation or cultural variant is expressed (e.g., who expresses it) and those that use the ‘content’ of trait or representation to determine whether to adopt it (Henrich and McElreath 2003).

Context-based learning mechanisms allow learners to use cues to selectively attend to and learn from certain members of their social environment, or to integrate information from different models in specific ways. We briefly describe two of these. The first (Henrich and Gil-White 2001) proposes that cultural learners use model-based cues to figure out who, among their potential models (those from whom they *could* learn), are most likely to possess adaptive information (i.e., mental representations) suitable to the learner’s current situation (e.g., his/her role in the social group). Theory suggests, and a wide range of empirical findings have confirmed, that both children and adults preferentially pay attention to and learn from models who are more skillful, competent, successful or prestigious (Hirschman 1982; Henrich and Henrich 2007; Birch et al. 2008; Nurmsoo and Robinson 2009; Chudek et al. 2011). Parallel reasoning and some evidence indicates that learners use cues of health, ethnic markers (dialect, dress, etc.), sex, and age in figuring out who to learn from (McElreath et al. 2003; Efferson et al. 2008; McElreath et al. 2008). These effects emerge early in childhood (Birch and Bloom 2002; Vikram 2004; Kinzler et al. 2007) and appear to influence cultural transmission across a wide range of representations, including

opinions, economic decisions, food preferences, strategies, beliefs, technological adoptions and dialect (Mesoudi 2008). Moreover, these biases appear to operate across domains of expertise, as experts or stars in one field or endeavor (e.g., basketball) are granted influences in other arenas (e.g., clothing choice or politics). Given this learning bias, a highly prestigious individual motivated by self-interest could express an opinion, belief or preference different from her own, that—once adopted by others—could yield benefits to her and costs to the learners (Henrich 2009).

A second mechanism, termed *conformist transmission*, focuses on how learners can best weigh and integrate observations from multiple models (Boyd and Richerson 1985; Nunn and Wantchekon 2011; Nakahashi et al. forthcoming). Learning mechanisms that ‘copy the majority,’ ‘average what most prestigious individuals are doing,’ or otherwise blend information from different models allow learners to effectively aggregate information across models and reduce transmission noise (i.e., errors introduced during the process of observation and inference in learning). Such processes allow learners to extract behaviors that are more adaptive, on average, than anything learners could acquire from a single model, or figure out on their own. Some empirical work supports these formal predictions (Kohler et al. 2004; Carpenter 2004; Coultas 2004; McElreath et al. 2005; Efferson et al. 2008; McElreath et al. 2008).

Alongside such context biases, evolutionary approaches to cultural learning also provide a rich set of cognitively-informed hypotheses regarding how the content of representations influences their transmission. The general insight is that learners should pay particular attention to and remember cultural representations likely to contain adaptive information. Specifically, cultural learners should be more likely to pay attention to and store representations when these are judged, *ceteris paribus*, more (1) fitness relevant, (2) potentially useful, and (3) plausible or compatible with evolved intuitions or existing cultural beliefs how the world works (Henrich 2009). Regarding the first, natural selection should favor more attention and recall for representational content of greater relevance to fitness, at least in ancestral environments. Often such content sparks more positive or negative emotional responses, thus adaptively biasing memory storage and recall. Empirical evidence for such content biases in learning has emerged in the domains of meat (Fessler 2003), gossip and social interaction (Mesoudi et al. 2006), disgust (Heath et al. 2001), and dangerous animals (Barrett and Broesch, in press). Most important for this discussion, O’Gorman and colleagues (2008) have shown a memory bias for information about social norms, over other kinds of information.

The Emergence of Norms and Institutions

The next step is to place these evolved learning strategies into game-theoretical models that permit different kinds of social interactions with other individuals who are also trying to adaptively learn. Any stable equilibria that emerges creates a reliable behavioral pattern for a given group or population. This effectively connects aspects of evolved cognition with higher-level sociological formations—stable equilibria are emergent, group-level characteristics. For many kinds of social interactions, the adaptive learning processes result in a multiplicity of stable equilibria, meaning that initial conditions and contingency are required to explain why any particular group ends up at one or another institutional form. This situation is beginning to look a bit like emerging social norms and institutions, at least in that these empirically-grounded evolved learning heuristics give rise to stable statistical regularities in social behavior that vary across social groups (Boyd and Richerson 1992).

The situation gets even more interesting when one considers social interactions in which individuals can exploit others by stealing from them or not helping them in a manner that is contingent on their behavior in a public goods situation, or common pool resource dilemma. Cultural evolutionary models show that if individuals are using the above-mentioned adaptive learning heuristics, then prosocial or group-beneficial norms of cooperation, collective action, or exchange (or not stealing) can be maintained, even when the possibility of repeated interaction is low, or the future time horizons of individuals differ (Boyd 1992). In sustaining such group-beneficial equilibria, these approaches provide solutions to the well-known second, third, etc. free-rider problems by (1) permitting the learning of strategies that punish non-prosocial behavior (Henrich and Boyd 2001; Boyd and Richerson 1992), or (2) linking non-prosocial behavior to players' behavior in another type of interaction (Gintis et al. 2001; Panchanathan and Boyd 2004; Henrich 2009). One problem with these 'prosocial solutions' is that these same incentivizing mechanisms—reputation, punishment and signaling—can stabilize any equally costly behavior, independent of its benefit to the group. Such mechanisms can, for example, stabilize behavior that hurts both individuals themselves and their group as a whole.

This oddity is a feature not a bug in this approach, as now these emergent phenomena are looking even more like the norms and institutions described by social scientists: we have behavioral regularities stabilized by either direct punishment or other incentives (through reputational damage) that are sometimes, but need not be, prosocial or group-beneficial. Some of these norms are maladaptive for individuals and groups (Durham 1991; Edgerton 1992). Thus, this approach meets the challenge of explaining why the same

mechanisms that sustain the institutions of collective action and cooperation also sustain maladaptive practices.

Why Internalized Norms

Norms are usually emotionally salient. At least some norms include an acquired component of internal motivation. People, at least in some groups, have internalized the performance of the norm as an end in itself. Economists would say these individuals have put the performance of the norm into their objective function. Adhering to a norm—a notion of how one ought to behave—can become a goal in itself (Camerer 2003).

To approach this issue, an evolutionary analysis is focused on the costs of information processing and making errors (violating norms), the temptation to seize immediate rewards, and the developmental circumstances of the adapting child. The issue of internalization has not been the subject of much modeling, so the materials below represent merely three suggested avenues. We do know, however, that internalizing acquired motivations is one of natural selection's tools, as people can internalize food preferences merely by observing others enjoying something (Birch 1987, 1980; Adnessi et al. 2005).

First, natural selection could favor internalizing norms as ends in themselves if this saved on information processing costs and/or the associated errors. If an institution exists and possess sufficient incentives for adherence, an individual might be better off to 'just do it' each time rather than performing an analysis for each slightly different situation that would involve considering the probability of getting caught violating the others' expectations, the likely penalty, the long-term reputation damage, etc. Moreover, suppose that each time one runs a mental calculation like the one just described, actors occasionally make errors that statistically lead to more sanctions. Internal motivation could help avoid unnecessary calculations, and avoid the errors of an inherently noisy environment. This, however, does not imply that an internally motivated individual never goes ahead and runs the complete mental calculation.

Alternatively, internally motivated adherence to norms may be natural selection's way of psychologically overcoming the pull of immediate rewards vs. long-term costs. Selection might act on cultural or genetic variation, or perhaps more likely, on a complex mixture of both. If people overweight immediate rewards compared to rewards amortized over years (and we often do: Berns et al. 2007), then internal motivation might provide that extra push to forgo the short-term gains in favor of long-term payoffs. Now, of course, natural selection or learning could fix this problem by adjusting our temporal discounting. Since many animals have the same discounting problem, and it

may be adaptive for other reasons, the internal motivation avenue may have been less costly.

Finally, when organisms live in rapidly changing or variable environments vis-à-vis genetic evolution, allowing proximate motivations to be internalized by learning, especially during development, can help the organism make adaptive decisions. Consider the acquisition of social norms from the perspective of children. Since norms vary among groups but are generally locally stable (at least over an individual's lifetime), they represent local environmental regularities that children can adapt to by rapidly adopting and partially internalizing the local norms, thereby avoiding sanctions. The costs and benefits of alternative actions, which often emerge gradually over time (if at all) can be evaluated while the individual continues to operate effectively in the social environment. The problem of making errors when cost-benefit calculation is used is particularly acute for children, since they lack the information possessed by adults to evaluate the consequences. Developmental work suggests that by adolescence, and often long before, children have solid knowledge and some internalization of many local norms. Children first acquire local norms in contextually specific circumstances and then rigidly apply them while gradually calibrating their understanding of the norm's domain of applicability using observation and experience (Lancy 1996; Fiske 1998; Harbaugh and Krause 2000; Harbaugh et al. 2002; Sutter and Kocher 2007; Rakoczy et al. 2008; Lancy 2009).

Experimental Support for the Cultural Acquisition and Internalization of Norms

Substantial experimental evidence—both old and new—indicates that people not only readily acquire norms via cultural learning, but that they internalize them. Since our interests here involve behavior related to collective action, we note that a long line of experimental research in the 1960s and 1970s with children show that context-specific prosocial norms for altruistic behavior toward strangers are readily acquired by observing others. Such experimentally-induced behavioral effects are not ephemeral and endure in re-tests months later (in which no observation of altruism occurred). Compared to both direct instruction and exhortations to 'give' by adults, opportunities for imitation of a charitable model showing positive affect have proved the most effective means to induce durable giving to anonymous others in children. Direct rewards, of course, could induce 'giving' as long as they remained available. However, unlike in the modeling case, 'giving' disappears as soon as the rewards do. Moreover, children also spontaneously scolded young children who did not behave altruistically once they had observed the behavior in a model, suggesting the mere observation of costly behavior spontaneously

induces a normative inference. Recent work with younger children shows that (1) children spontaneously infer the existence of social norms, in one trial learning, (2) react negatively to deviations (norm violations), and (3) monitor others for emotive cues of proper behavior (Rakoczy et al. 2008; Fusaro and Harris 2008). Such findings suggest that our minds are built to expect a world with norms and institutions (Chudek and Henrich 2010).

A variety of evidence suggests that behavior experiments, such as the Ultimatum Game, measure social norms that have evolved culturally to govern exchanges in ephemeral interactions. Developmental evidence indicates that these norms are acquired only gradually over the first two or three decades of life. In Dictator and Ultimatum Games, Western children's offers do not begin to approach adult levels until around age 12, followed by a slight drop during adolescence when they learn to break the fairness norm. After adolescence, mean offers continue to increase again through the university years, not reaching the adult plateau until about age 25 (Carter and Irons 1991; Harbaugh et al. 2002; Carpenter et al. 2005; Bellemare et al. 2008). In the Dictator Game the differences between students and fully socialized adults is dramatic. In the Ultimatum Game, in which the responder can punish low offers, giving the lowest positive offer is the income maximizing strategy because adolescents' willingness to punish have not risen sufficiently high to discourage unfairness. By full adulthood, the modal offer and the income maximizing offer have converged on a 50/50 split. Similarly, experiments using the Trust Game in Europe show that the adult plateau is not reached until the mid to late twenties (Sutter and Kocher 2007).

Our theoretical approach to norms gives us a means to anticipate and theorize about how different contextual cues in laboratory experiments, which do not directly impact the payoffs structure of the game, can influence game play. Subjects arrive at experiments equipped with norms, which include contextually specific beliefs (expectations of others behavior) and preferences, and then face novel situations (Anderson and Putterman 2006; Ones and Putterman 2007; Putterman n.d.). They have to figure out how to behave, in part, by figuring out which—if any—of their norms apply in this situation. Since most experimental games involve both money and anonymity, players from societies with norms that apply to such contexts will be influenced by both their norm-related beliefs and their internalized motivations (Henrich et al. 2004).

Similarly, setting up 'framed' games with identical payoff structures but different accompanying story lines, such as a 'Wall Street' game versus a 'community' game (Ross and Ward 1996), yields somewhat different allocations among university students because they probabilistically cue different norms (also see Pillutla and Chen 1999). Similarly, Hayashi et al. (1999) show that

simple framing differences strongly affect rates of cooperation in an otherwise identical two-person prisoner's dilemma, and that these effects depend on whether one is from Japan or the U.S. This finding fits with observed differences between the U.S. and Japan in non-experimental contexts. Such cultural differences in framing effects reflect the degree to which the same context cues different norms in different places.

From this point of view the prosocial effect of pre-play communication results from the players ability to establish a coordination of norms under circumstances in which there is ambiguity about what norm applies to a context (Ostrom et al. 1994).

It bears emphasis that we do not think that 'norms' are the only thing influencing play in experimental games. Aspects of the games, such as the material costs and benefits, opportunities to cultivate a reputation, and the prospects of repeated interaction ought to influence game behavior in predictable ways, consistent with either evolutionary considerations or rational choice (Henrich and Henrich 2007). Some seemingly contextual effects—effects that do not influence the actual payoff structure—may influence game play by influencing players' perceptions of the possibilities for reputation formation, repetition (Haley and Fessler 2005), or their conclusions about which norms are applicable. Interesting, there is reason to suspect that subject-experimenter anonymity has little impact on experimental game findings (Barmetter et al. 2011).

Work in neuroscience and neuroeconomics has recently contributed to this line of research by showing that behaving in the manner demanded by local norms, by cooperating, contributing, or punishing in locally prescribed ways activates the brain's reward or reward anticipation circuits in the same manner as does obtaining a direct cash payment (Sanfey et al. 2003; Rilling et al. 2004; de Quervain et al. 2004; Fehr and Camerer 2007; Tabibnia et al. 2008). It seems that complying with local norms by cooperating, contributing, or punishing 'feels good' to brains in the same way that personally getting money does. Several other results are convergent: (1) cooperating and getting money (from the cooperation) feels better than just getting the same amount of money; (2) punishing by really hurting defectors (physically or monetarily) activates these reward circuits more than punishing symbolically; (3) receiving money also activates the same reward circuits as giving money to charity (Harbaugh 2007); and (4) activations of the brain's reward circuitry in these experiments predict behavioral outcomes. These insights combined with the fact that behavior in such experiments varies dramatically across human societies, and that chimpanzees do not behave prosocially in such experiments (Silk et al. 2005; Jensen et al. 2006, 2007a, 2007b; Vonk et al. 2008), suggest

that this perhaps uniquely human circuitry drives the ontogenetic acquisition of and internalization of social norms.

Convergence with Rational Choice and Economics

Evolutionary and economic approaches have begun to converge on both a unified conception of learning and a theoretical foundation for social norms. Aoki (2001: 194-7) has a particularly clear argument about the complementary nature of classical and evolutionary game theory. By considering both the impact of incomplete information and uncertainty on rational decision-making and the effectiveness of simple, 'ecologically rational' heuristics for dealing with complex situations, approaches to bounded rationality are assembling an understanding of human social behavior that parallels that derived from evolutionary theory. Economists have shown, for example, that copying the successful people or copying the majority are—under particular conditions—quite rational (Ellison and Fudenberg 1993; Spencer and Huston 1993; Weibull 1995; Schlag 1998, 1999), as well as fitness-maximizing (Nakahashiet al. forthcoming). Such strategies are rational when information is costly to acquire or process, or when information about the costs and benefits of alternative behavior are noisy (error ridden)—circumstances common to many real life decisions. Economists have also led the way in exploring bounded learning strategies based on direct experience (Young 1998).

Theoretical models that place individuals deploying these learning strategies in social interaction show stable behavioral patterns that look like norms. This is not surprising in some cases, since the underlying learning heuristics are similar to those used by the evolutionary theorists, but in other cases it does robustly re-affirm that adaptive learning plus social interaction can yield a wide variety of fairly stable outcomes. This multiplicity of stable outcomes is even a feature of classical game-theoretical models that assume perfect and free information and processing power—a finding enshrined in the folk theorem (Fudenberg and Maskin 1986).¹

Within economics, the emerging focus has led to important experimental work on learning in social interactions. The experiments confirm that, at least in laboratory experiments, learners do appear to be using learning heuristics like 'copy the successful' as well as experienced based learning rules (Pingle 1995; Offerman et al. 2002; Alpesteguiat et al. 2003). Many of these findings

¹ The social norms that arise from learning and social interaction are at least dynamically stable in the vicinity of the equilibrium behavior (when most people are sticking to the norm). Since dynamically stable equilibria are usually also stable in classical game theoretic models (given typical equilibrium concepts) in which actors are fully rational, selfish and omniscient, norms can persist even when some members become better informed and begin to approach full rationality.

converge with findings from both social psychology and development psychology, derived using quite different experimental tools (Chudek et al. forthcoming), as well as with field observations from diverse societies (Henrich and Henrich 2007; Reyes-Garcia et al. 2008; Henrich and Broesch 2011).

In returning to ideas discussed by Adam Smith and other classical scholars (Hirschman 1982), economists are beginning to explore the internalization of norms, or endogenous preference formation, and have specifically considered the effect of markets. Rather than waving off the question of where people's preferences come from, an increasing number of economists are examining the possibility that preferences emerge in part from interaction with the local institutional environment (Bowles 1998; Alesina and Fuchs-Schundeln 2007; Nunn 2008). People's motivations or preferences are partially calibrated to performing the local equilibrium (Francois and Zojojnik 2005; Nunn and Wantchekon 2011; Nunn, in press). Some economic historians argue that those who subscribe to social norms do so in part through a moral imperative because they believe it is the right thing to do. This is an important point not only because it adds more regularity to behavior, but also because it makes norms self-enforcing. As Greif (2006: 37) puts it, "internalized norms are socially constructed behavioral standards that have been incorporated into one's superego (conscience), thereby influencing behavior by becoming part of one's preferences." Even textbooks in microeconomics now take this possibility seriously (Bowles 2004).

One explanation for internalized motivations in economics parallels the above evolutionary explanation based error management. If norm violations result in sanctions or mis-coordinations, but certain situations may tempt one to violate a norm (by e.g., not tipping), individuals should develop internalized motivations (i.e., preferences) that allow individuals to avoid norm violations that will cost them in the long run (Frank 1988).

Empirically, some of the best evidence for the importance of culture and norms comes from economics. A growing body of empirical work in economics reveals the importance of cultural or epigenetic inheritance in sustaining and explaining much human social behavior, including domains such as the importance of family ties (Giuliano and Alesina 2010), impersonal trust (Guiso et al. 2006; Algan and Cahuc 2010), and corruption (Fisman and Miguel 2007), as well as other domains like violence, fertility and hard work (Fernandez and Fogli 2006, 2009; Guiso et al. 2006). By linking cultural beliefs or behavioral practices of the descendants of immigrants to the U.S. or Europe back to their countries of origins, these analyses demonstrate the durability of these beliefs, motivations, and practices in a manner inconsistent with cost-benefit analysis or developmental adaptations. By further showing that they these effects dissipate after a few generations of assimilation, such

evidence suggests that genetic differences among populations are unlikely explanations. Culture creates measurable historical inertia, but not as much inertia as genetic inheritance does.

Multiple Mechanisms of Norm Stabilization

Cultural evolutionary models of cooperative institutions illustrate the potential for numerous alternative routes to stable cooperative institutions, each involving some combination of reputation (Panchanathan and Boyd 2004), signaling (Gintis et al. 2001; Boyd et al. 2010), costly punishment (Axelrod 1986; Boyd and Richerson 1992; Henrich and Boyd 2001; Sigmund et al. 2010), costly rewarding (Kendal et al. 2006) or particular forms of cultural learning (Henrich 2009). For example, Panchanathan and Boyd (2004) show how individually costly norms can be stabilized by attaching players' reputations in a dyadic helping game to their reputations in a larger-scale individually costly interaction. If an individual fails to cooperate in the larger interaction he gets a 'bad reputation' and other individuals can withdraw their help from him in the two-person game *without* getting a bad reputation themselves. Otherwise, individuals who refuse to help those with good reputations in the two-person helping game get a bad reputation. There is no free-rider problem here because individuals 'sanction' by withdrawing help, and thereby not paying the cost of delivering help (Eldakar and Wilson 2008).

Analyses of these alternative incentive configurations show similar properties. All yield multiple stable equilibria and can stabilize any costly behavior, independent of whether the behavior delivers benefits to anyone. Most, though not all, require a well-functioning reputational system, which limits the size of population in which they can sustain costly behaviors. The emerging picture, consistent with the folk theorem, is that cultural evolution may be capable of harnessing and extending our evolved psychology to construct a myriad of different institution-sustaining mechanism.

A problem with the multiplicity of proximal mechanisms for sustaining equilibria is that the different mechanisms and equilibria likely exhibit a wide range of functionality. We can imagine several mechanisms by which dysfunctional norms/institutions can become established. Exogenous changes may make an institution obsolete, yet it may be sustained by the mechanisms we have reviewed. The search for new equilibria by rational or evolutionary means will tend to be constrained by history (Greif 2006), leading to many systems reaching only suboptimal equilibria. Predatory elites and other self-interested subgroups with some form of coercive power may be able to establish equilibria that disproportionately benefit them. Ideologically motivated groups with coercive power may sustain equilibria at mad extremes, at least for brief periods of time.

Solving the Equilibrium Selection Problem

Once a combination of expectations, motivations, and beliefs converges in a group to create an institution, we have a somewhat sticky situation. If many different societies, or groups, converge on different locally stable social norms/institutions, due to the aforementioned path-dependence and historical specificity, is that it? This problem is made even more poignant by the fact that many different norms can be stable, and most of these are not prosocial or group-beneficial. So, all we have is a population of varying groups, all with different norms, only a few of which involve any prosociality. Is there any way to select among these norms? This is the problem of *equilibrium selection*, a serious problem that emerges in both dynamic evolutionary approaches and those rooted in static rationality.

Three broad theoretical approaches confront the problem of *equilibrium selection* (Henrich 2006). The first, and perhaps the most intuitive, is that rational forward-looking individuals will recognize the long-term payoffs available at stable cooperative equilibria, assume others are similarly sensible, and choose the prosocial state (Harsanyi and Selton 1988). This is certainly possible, and likely to be important in some circumstances. However, three things are worthy of consideration. First, groups may sometimes appear to systematically consider various alternative behaviors, and select one that works. But, if groups are generally bad at foreseeing the outcomes of complex dynamic processes (which they certainly are), then these reasoned decisions may be essentially random selections vis-à-vis group beneficial outcomes. It may be that when groups get lucky, we credit them with insight and reason. The empirical record suggests that attempts to engineer social change are at best only partially successful. Burke's (2002) textbook *Organizational Change* begins chapter 1 with the bald statement "Most efforts by executives, managers and administrators to significantly change the organizations that they lead do not work." Second, group decisions are often heavily influenced by leaders and coalitions with interests that diverge from the overall group (Ensminger and Knight 1997). Third, as one looks across the globe, the world is still full of non-prosocial and even downright anti-social institutions that hurt the group as a whole (Edgerton 1992). Nevertheless, these mechanisms are not mutually exclusive, and this kind of mechanism may still be part of the story. Groups may sometimes change norms quite consciously by meeting and reaching consensus, although actual cases suggest that they consciously adopt the norms of other more successful groups, making this a form cultural group selection, see below.

The second approach is based on the stochasticity inherent in any interaction. Different stable equilibria (norms) are more or less susceptible to this stochasticity, meaning that in the long-run some equilibria will be

substantially more common than others (Young 1998). That is, over the long-run some norms will be more likely to collapse, and cause the group to evolve to a different norm. Under some conditions, stochasticity may favor either more prosocial (highest mean payoffs) or more equitable (more equal division of production) equilibria, but this need not be the case (Young 1998; Kendal et al. Aoki 2006). We might expect that less functional equilibria will excite more individual and group resistance, leading to their frequent breakdown. By contrast, more functional equilibria are likely to excite less individual exploration and less resistance and rebellion. However, the ability of people to know they are at a less functional equilibria often depends on knowing groups exist at more functional equilibria. Much like trial and error learning, social groups may explore the space of nearby possible equilibria and to tend to find better ones through a reinforcement-like process at the collective level (Greif 2006). To the extent that this learning like process is calculated and forward looking it will converge on the rational search described above. To the extent that learning relies on copying more successful groups, it converges on the next process, cultural group selection.

Our third equilibrium selection mechanism, cultural group selection, gives priority to the competition among social groups, who have arrived at different institutional forms. Inter-group competition favors the spread of individuals and/or practices from groups stabilized at more prosocial equilibria (Boyd and Richerson 1990). In humans, competition between groups can take the form of warfare, demographic production, or more subtle forms in which individuals learn decisions and strategies by observing higher-payoff individuals—some of whom are from groups with more group beneficial institutions (Henrich 2004). This can lead to a differential flow of decisions, strategies, and even preferences from higher to lower payoff groups (Boyd and Richerson 2002), or to the differential migration from high payoff groups to lower payoff groups (Boyd and Richerson 2009).² Some organizations of complex societies

² Those less familiar with evolutionary thinking might question whether all of these examples of equilibrium selection process should be categorized under cultural group selection. We think two key requirements are relevant to defining a process as a form of *cultural group selection*. The first is that the relevant behavior be influenced by social learning—that's the 'cultural' part. The second, and less well understood, requirement arises from how evolutionary processes can be partitioned into that component of change driven by the variation within groups and that component of change driven by the variation between groups. Since institutions within groups are typically stable, the within group component will often be small. Since it's the difference in payoff between groups that are then driving the change (based on the variation between groups), it's group selection according to generally accepted definition laid out in 1972 by George Price and presented in textbooks (McElreath and Boyd 2007).

(business firms, trade diasporas, voluntary associations, cooperatives, religious communities and so forth) thrive while others fail and disband. To the extent that such either organizations survive or are preferentially imitated by other organizations, cultural group selection could be quite strong (Alchian 1950). Also, thriving firms may be a source of innovations in adaptive norms/institutions that spread to other organizations and perhaps become general in a society (Klepper 2009).

Importantly, even if these mechanisms do not entirely inhibit the invasion of defecting strategies, prosocial norms can still often spread in structured populations with inter-group competition because such mechanisms tilt the balance of within vs. between group evolutionary forces in favor of prosocial norms (Boyd et al. 2003; Guzman et al. 2007; Boyd et al. 2011).

Different forms of cultural group selection have quite different properties. For example, when whole societies or other large organizations compete militarily, the group selection process is relatively slow (on the order of a millennium) and easily breaks down if ideas can spread piecemeal among groups (Soltis et al. 1995). This second property means that good ideas from one society are not easily mixed with good ideas from another. On the other hand, when differences in group performance lead to selective borrowing or selective migration, the group selection process can be much more rapid and can lead to extensive recombination (Boyd and Richerson 2002; Boyd and Richerson 2009). Institutions may be influenced by both of the above processes, but since culturally acquired beliefs and values are often integrated, at least partially with other institutions and religious beliefs, the processes can be slow and constrained to certain paths. Thus, Russia underwent two wrenching revolutions in the twentieth century, only to emerge in the early twenty-first century with an authoritarian regime with an uncanny resemblance to the nineteenth century Czarist regime (Ross 2005).

Virtually all of the theoretical work by evolutionists to date consists of models with various kinds of limited rationality on the part of individual actors combined with selective forces of various kinds that act on behavior blind to whatever forces generate the variation that selection acts upon. Applications to situations where individual actors combine to make decisions about changing norms in some sort of collective political system are very few. Roemer (2004) gives an example of what direction such investigations might take. Greif (2006) gives an appealing sketch of how norms/institutions might evolve. Institutions that historically have been stable solutions to organizational problems are often destabilized by internal or external changes. For example, a successful long-distance trading system in which honest behavior is stabilized by word-of-mouth reputations and ostracism of miscreants may be undermined by its very success. The growth of the system may make word-of-

mouth reputations hard to accurately acquire. Rich, busy traders also begrudge the time required to determine reputations by word of mouth. Once such a system is destabilized, participants will employ a collective decision-making process that engages in a search for a new equilibrium. Such a search will be limited by the history and culture of the participants rather than an exhaustive assessment of all the possible equilibria. In other words, a collective search for a new equilibrium will suffer the same sorts of uncertainties, limited information, and unintended consequences as individual efforts at rational decision-making.

Those with an interest in policy innovations will have detected a note of pessimism here. Attempts to change norms will often fail (think of the War on Drugs) and successful attempts to change them often results in unhappy and unintended consequences as in so many attempts to improve organizations noted by Burke (2002). The lesson of many studies is that historical solutions to commons dilemmas very often work better than those generated by top-down design (Ostrom 2002). Deliberate policy innovation is perhaps most likely to be helpful when institutions have become destabilized or when a 'sick society' is demonstrably at an inferior equilibrium. Perhaps policy makers ought to bear Galen's injunction "first, do no harm" in mind. We think that understanding the processes of cultural evolution promises to help policy makers improve on their poor record of institutional design (Richerson et al. 2006).

Building on a foundation of formal models and computer simulations, there are now many lines of empirical evidence to support cultural group selection, including data from laboratory studies, archeology, history, and ethnography. In the laboratory, Gurerk et al. (2006) have shown how individuals migrate from lower payoff institutions to higher payoff ones, and adopt the local norms of that group. Atran et al. (1961) have shown how conservation-oriented ecological beliefs spread from locally prestigious Itza Maya to Ladinos in Guatemala, and how highland Q'eqchi' Maya, with tightly bound cooperative institutions and commercially-oriented economic production, are spreading at the expense of both Itza and Ladinos. Soltis et al. (1995), using quantitative data gleaned from New Guinea ethnographies, has shown that even the slowest forms of cultural group selection (conquest) can occur in 500 to 1000 year time scales. Using ethnohistorical data, Kelly (1985) has demonstrated how differences in culturally acquired beliefs about brideprice fueled the Nuer expansion over the Dinka, and how different social institutions, underpinned by norms underpinning segmentary lineage organizations, provided the decisive competitive advantage. Similarly, Sahlins (1961) argued that cultural beliefs in segmentary lineages facilitated both the Nuer and Tiv expansions. Recent work suggests that religion and rites that

galvanize group solidarity and deepen commitment spread by cultural group selection (Henrich 2009). At the global level, Diamond (1997) has made a cultural group selection case for the European expansion after 1500AD, as well as for the Bantu and Austronesian expansions. Using historical data, Turchin (2006, 2009, 2010) has argued for the importance of cultural group selection in the formation of large empires between about 3000 BCE and 1800 CE. Applying basic principles from this approach, he is able to predict the geographic distribution of mega-empire formations and the cycles of growth and decay of cooperative institutions. Using archeological data, anthropologists are increasingly arguing for the importance of cultural group selection in prehistory (Flannery and Marcus 2000; Spencer and Redmond 2001), including competition among foragers (Young and Bettinger 1992; Bettinger and Baumhoff 1982). In the modern world, recent work examining the effect of increase competition among organizations show that greater inter-group competition predicts greater trust (Francois and van Ypersele 2008). This causal demonstration is consistent with comparative experiment work linking market integration to measures of fairness from three behavioral games (Henrich et al. 2004, 2010).

Culture-Gene Coevolution as the Origin of Our Tribal Instincts

To understand the unique nature of human sociality, let's first consider the social life of chimpanzees, the best studied of our two closest cousins (the other is the bonobo). In recent decades, much effort has been directed at the study of chimpanzee social life using both observational and experimental techniques. Compared to many animals, even other primates, chimpanzees in the wild cooperate in many ventures, such as aggressively expanding the group's territorial boundaries at the expense of neighboring groups (Mitani et al. 2010). Nevertheless, compared to most human groups these ventures are rather modest. Most cooperation is between male dyads most of whom are not close kin, at least in one well studied group (Langergraber et al. 2007). The appearance of chimpanzees from neighboring groups generates fear, hostility, and frequently violence (Manson and Wrangham 1991). Human hunter-gatherers, by contrast, maintain large networks of kin and non-kin, even in the smallest scale human societies (Wiessner 1983, 1982; Hill et al. 2011). The members of the ethnolinguistic tribe, ranging in size from a few hundred to a few thousand people, can generally organize cooperative ventures, if opportunities present themselves, and can sustain peaceful, mutually beneficial transactions. Cross-tribal ties are not uncommon, resulting in trade, alliance, and a fair frequency of intermarriage.

Experimentalists have also been working to map the similarities and differences between chimpanzees and humans. Experimental studies of cooperation in chimpanzees suggest that individuals view social interactions as mainly competitive, and routinely pass up opportunities to provide aid to others even at extremely low or no cost to themselves (Hare and Tomasello 2004; Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008).³ Perhaps the most telling fact about performing behavioral experiments with chimpanzees is that it is impossible to perform the equivalent of the typical human experiments, which usually invite strangers to exchange or interact. The mere sight of an unknown chimpanzee sparks fear, hostility, and aggression. Humans treat other humans not known to be a threat, or not obviously a member of a group assumed to be hostile, as potentially cooperative. Chimpanzees treat any individual not known to be an ally as presumably hostile.

We argue that cultural evolution sparked and drove self-domesticating process. This occurred in our species, and not others, because humans possess psychological abilities and motivations that generate high fidelity cultural transmission in a manner not observed in other species. While chimpanzees do reveal some social learning abilities, they do not possess anywhere near our species' capacity for cultural transmission, and its consequent cumulative cultural products (Tomasello 1996; Whiten et al. 2004; Horner and Whiten 2005). The idea that complex culture can fundamentally alter the evolutionary process is resisted by some evolutionary biologists and evolutionary social scientists because it seems to violate the idea that a supposedly proximal phenomenon like culture cannot be an ultimate evolutionary cause. Laland and colleagues (2011) show that culture and other proximal processes in fact do have impacts on evolutionary processes.

Attempts have been made to raise infant chimpanzees as if they were humans (Kellogg and Kellogg 1933; Hayes 1951; Temerlin 1975; Fouts and Mills 1997). People undertaking these quasi-experiments imagined that chimpanzee infants would learn human norms and come to behave much like humans. Chimpanzees can indeed be taught many human behaviors, but by temperament they remain wild animals. Even youngsters of two years are strong, willful creatures that pick up human norms very slowly and incompletely. These results imply that humans are genetically predisposed to behave like humans and in particular to be prepared to acquire the norms that we use to operate our complex institutions and organizations (see discussion above: Rakoczy et al. 2008).

³ For a different view see de Waal (2008).

Our argument here is that the emergence of norms created a selection pressure on individuals for the cognitive abilities and social motivations necessary to survive in a norm-governed world, where deviation from local social norms can result in some form of social sanctioning. Competition among groups with different norms increasingly favored the emergence and persistence of group-beneficial norms—via cultural evolution—in groups larger than primate dyads. The primitive cooperation and sanctioning in these groups in turn selected for genotypes that were adapted to cooperate in such groups. Too-fractionious individuals might be driven from the group by collective action, for example (Boehm 1993, 2012). Repeated rounds of this gene-culture coevolutionary ratchet eventually resulted in a species that domesticated itself, so to speak.

The evolution of dogs provides a helpful point of reference for the process we have in mind. Humans were the selective forcing acting on ancestral wolves has eventually produced domesticated sub-species that possessed both motivation and cognitive abilities attuned to human behavior. For example, dogs readily understand human pointing while neither wolves nor chimpanzees do (Hare et al. 2002). Dogs, like small children, are relatively easy to train to follow simple human rules, and readily assume humans are providing information the dog should use (Topal et al. 2009). Wolves, coyotes, and chimpanzees (and very likely our ancestors at the time of the split of the human and chimpanzee lineages) are very different in this regard. We domesticated ourselves by the cultural evolution of institutionalized social selection much we domesticated dogs by selecting for an ability to follow our rules.

The evolution of humans from primate ancestors involved the evolution of sympathy, loyalty, and pride in one's contribution to the group. These qualities originally supported simple tribes in which food was shared, territory defended, and rules enforced without any top-down leadership. Just as organizations today with too many employees that look out for themselves tend to lose in competition with ones where more look out for the welfare of the organization, tribes with good norms and enough people willing to follow them triumphed over tribes with less effective norms, who had fewer individuals willing to follow or enforce them. By 'good norms' we mean social norms that effectively harness aspects of our evolved psychology in ways that led to success in inter-group competition. Modern cultural evolutionary theory and much evidence are consistent with the same basic idea. Group selection operates much more effectively on cultural variation than genetic variation (Bell et al. 2009). Thus, the fact that humans are both sophisticated cooperators and sophisticated social learners is not at all coincidental if we are correct.

The cultural and genetic elements of our social psychology interacted over the long run of human evolution. To judge from the stone tools humans left behind (unfortunately, a narrow window on past cultures), human cultural sophistication probably evolved in several waves after about 2.6 million years ago, long after our lineage separated from that of the other apes (Richerson et al. 2005). The picture is still hazy, but much seems to have happened in the past 250,000 years. Molecular evidence suggests that humans have undergone a burst of genetic evolution in the wake of the origins of agriculture and some controversial arguments hold that psychological traits as well as those related to disease and diet responded in a major way to the development of food production and the larger, more sophisticated societies it made possible (Cochran and Harpending 2009). In the end, we became the unique creatures we are—capable of enormous collective enterprises because of our ability to cooperate and trust conditionally, even though we are beset by conflicts on scales from the interpersonal to the international.

On the practical side, cultural evolutionary science sketches the nature of the human raw material and the kinds of evolutionary tradeoffs that constrain the design of organizations (Richerson and Boyd 1999; Richerson et al. 2006). It points to the levers that policy makers have over the norms and institutions that they might use to engender as much cooperation and as little conflict as is possible given our complex social proclivities. The advice that flows from the science of cultural evolution is as hard-nosed as any you will get from economists. It paints a rather softer picture of people's willingness to cooperate but emphasizes that our raw propensities are useless without well-functioning institutions. Our main claim both for cultural evolutionary theory and its advice to policy makers is that they have greater realism than other social science based approaches to management. Many of cultural evolution's theoretical insights come from models as straightforward as those classically based on the selfish rationality assumption.

Empathy and the Moral Hidden Hand

Our theory has a back-to-the-future aspect. Adam Smith and Charles Darwin both made empathy the cornerstone of their theories of virtue. They observed that without the other-regarding virtue of sympathy, the social life that humans enjoy today would not be possible, much less reforms aimed at improving our social life. Darwin gave sympathy and related everyday virtues an important evolutionary role in favoring good social rules and providing the basis for rejecting flawed ones. Market forces certainly do exert important hidden-hand effects, but the effects of everyday virtues are equally pervasive and nearly as hidden in the sense that formal legal institutions and formal policies and procedures represent only a small part of their effect. Informal

rules and everyday virtues of individuals affect our behavior in a multitude of unforced, unplanned ways. Approximately one percent of humans, psychopaths, lack the normal emotions of sympathy, loyalty, and respect for prestige. They cause enormous damage to the organizations they inhabit (Babiak and Hare 2006; Boddy 2011). Psychopaths behave in a highly selfish manner and engage in attempts to dominate others through bullying and deception. Intelligent psychopaths are often successful in reaching leadership roles in organizations where they are often highly destructive (think Bernard Madoff). It is hard to imagine human social systems functioning as they do if most, or even a substantial minority, of humans were psychopaths. Our societies would resemble the small dominance-structured troops so common in other primates. Formal law is used to control psychopaths and other miscreants but it is costly and cumbersome, and is most often invoked when custom and everyday virtue fails in some way. Interestingly, it may be that market competition actually favors such morals and virtues (at least certain kinds: Henrich et al. 2010).

Smith's and Darwin's old insights are buttressed by modern theoretical and empirical studies, referred to above, that show both how human behavior deviates from the self-regarding assumptions and how those patterns vary across human societies. The canonical model from economics fails in all societies studied, but fails in different ways in different places (Henrich et al. 2005, 2010; Herrmann et al. 2008). Given such results, we should not be surprised that businesses attending to their social and environmental responsibilities, conservatively speaking, make no less money than the average business and in many cases seem to make more money than ones that focus ruthlessly on the bottom line (Orlitzky et al. 2003). Nor should we be surprised that village-scale commons are frequently well managed on the basis of locally evolved norms/institutions (Ostrom 1990). Indeed, the Lockean liberal political theories that so influenced Smith and Darwin are at least as much about the moral hidden hand as the market hidden hand (de Toqueville 2005; Putman et al. 1993).

The moral hidden hand likely biases our decisions about what norms to adopt. Most of the time, individuals are in the grip of traditional norms and institutions that circumscribe their ability to act directly on prosocial impulses derived from the social instincts. We normally think of norms mostly being about steering individual behavior away from a selfish human nature in prosocial directions, but the opposite is common. Consider a slave-owning society. Empathy with slaves might tempt many people to treat slaves as ordinary human beings. Slave owners in a slave-owning society cannot contravene the laws and customs regulating slavery except perhaps at the margin. When choices about new institutions are on the table, then individuals

have choices about what norms to advocate, what laws to vote for, or what societies to migrate to, and these choices will tend to be influenced by the moral hidden hand. Thus, the coevolutionary process has somewhat lightened the load that must originally have been directly on cultural group selection. Once the coevolved prosocial instincts were in place they ought to have accelerated the evolution of norms and institutions that better and more often solve dilemmas of collective action. The process is far from perfect, of course.

The notion of cultural evolution also strikes us as a way to put the debates of conservatives and radicals in the Lockean tradition on a sounder scientific footing (Haidt 2012). Radicals are right to point out that adaptation requires change, and sometimes might justify the pursuit of large changes. Conservatives are right to point out that existing norms/institutions may perform a social function that participants themselves don't understand. Too-bold attempts at reform may well destroy more useful norms/institutions than they create. The effects of wholesale changes in norms and institutions are hard to carry off and the results are hard to predict. The practical policy maker sees a tradeoff. Small policy changes have fewer unforeseeable uncertainties than large ones, and hence are to be preferred, all else equal. On the other hand, norms/institutions may be stabilizing a clearly suboptimal equilibrium and at other times a traditional equilibrium may have broken down. Bold measures may be required, risks notwithstanding. The same practical policy makers may look more radical or more conservative depending on such tradeoffs.

Often, the optimal policy is quite unclear despite the best analysis. One of the most important lessons of liberal political regimes is that they provide a relatively benign system where organizations are easily formed, and can foster their own norms and institutions. But they must compete for members, financial resources, and the like. Members of clubs can vote with their feet. Business firms can prosper or go bankrupt. Citizens can migrate from one state to another. Policy analysts and policy makers can sort through these experiments for the causes of success and failure. The Schumpeterian process of creative destruction need not be too brutally destructive, at least compared to the cases in which success and failure are judged on the battlefield and the losers killed or enslaved.

Human organizations are complex systems that function best when the moral hidden hand is fully harnessed and when existing norms/institutions are well adapted to our moral sense. A private firm, government bureaucracy, NGO, neighborhood, or village full of high-morale cooperators will tend to be economically efficient and perhaps will have some care for objectives like social justice and environmental protection. The organization that focuses excessively on its narrow self-interest may find that it has inadvertently

handicapped the moral hidden hand by encouraging members to be selfish, which might include diverting organizational resources for their own gain by focusing on personal agendas, padding expense accounts, pilfering the public purse, stealing water from the common canal, and by the many other ways that selfish people can exploit the organization (Bowles 2008). Most economists are surprised by findings, such as Orlitzky et al.'s (as they are by many of the cultural-evolutionary findings that underpin our analysis). Economists have been trained to expect a *tradeoff* to exist between a firm's profitability and any *special* attention it pays to social or environmental concerns rather than the *synergy* between these goals predicted by cultural evolution (and supported by laboratory experiments). Economics students, incidentally, are more resistant to the moral hidden hand in the laboratory than other students and have trouble making cooperation work (Carter and Irons 1991). Having imbibed the selfish rational assumption, they are handicapped in running the model businesses we set up in the laboratory. Economics, we should add, is changing very rapidly because some of the most elegant support for the moral hidden hand has come from the studies of pioneering experimental economists brought up in the neo-classical tradition (Guth et al. 1982; Frey and Jegen 2004; Camerer and Fehr 2006).

Our Tribal Nature, Work-Arounds, and Organizational Management

The understanding that human nature is fundamentally tribal is one of the important insights we believe evolutionary social science brings to the applied field of policy analysis. Even the most complex and hierarchical human organizations, such as modern armies, are broken down into units like squads, platoons, companies, and regiments in order to tap the human genius for using the moral hidden hand to forge adaptive norms/institutions and to operate them effectively. The management of human organizations is made possible, but not easy, by a tribal human nature that is conditionally cooperative. Given the right culturally transmitted norms/institutions and enough of our peers willing to honor them, most of us are also willing to honor them. Organizations succeed when they recruit the group favoring the tribal impulses that most of us have, but they also have to work against the fact that the constituent organizations of complex societies face a more constrained job than true tribes. Egalitarian tribes worked only for their members' benefit, whereas organizations in complex societies have a broad array of 'stakeholders' to satisfy—customers, suppliers, owners, lenders, voters, neighbors, and regulators. Such societies use grants of power and other devices as 'workarounds' to control inter-'tribal' anarchy in the interests of domestic tranquility and an efficient division of labor. But such workarounds often lead

to management problems, such as abuses of police power for selfish ends, a tendency of organizations to engage in costly contests rather than merely divide labor, the evolution of organizations with large ideological claims, and so forth (Richerson and Boyd 1999). Successful management is thus substantially the art of using work-arounds to tap the moral hidden hand while at the same time minimizing their inherent vices.

Key Summary Points for Students of Collective Action Problems

The theoretical and empirical lines of evidence are converging to suggest that institutions represent diverse and complex cultural-evolved contrivances that are built on, and sustained by, exploiting aspects of our evolved psychology, including both our tribal psychology and older aspects of our primate psychology such as those related to kinship, dominance and reciprocity. This implies that (1) there is no one solution to large-scale human collective actions (there are many) and (2) solutions are local, historically contingent, and context-specific. Moreover, some of these mechanisms involve interconnecting different kinds of social interaction, via reputation, and harnessing some of the darker aspects of our psychology (jealousy, status-striving, vengeance) to stabilize intuitions. This means efforts to stamp something that (everyone agrees) is maladaptive (witchcraft, theft, property damage) may collapse collective action by effectively throwing a monkey wrench into an interconnected machine (Chudek and Henrich 2010).

This recognition means that effective actions at particular location require an ethnographic study of how the local institutions function, and are sustained. The ‘natives’ may have such knowledge intuitively, but outside policy makers had better take care. Existing theoretical models can guide inquiry. One key is to figure out how the sanctioning system works. Once the system is understood, we can consider how to augment it, or tune it up. As noted, institutions ultimately exploit human nature. Here is a handy list of aspects of our evolved social psychology that one should keep in mind when repairing an institution, or building a new one.

- 1) **Kinship:** As humans, we seem naturally inclined to help our close kin. In small-scale societies institutions extend notions of kinship to distant kin and non-relatives, allowing our innate kin biases to guide and inform both our treatment of relations within the kinship system and guide the judgment of other behavior within the system. People clearly know the difference between their real and metaphorical brothers, but calling him a ‘brother’ tells him and everyone else how you are supposed (normatively) to treat him. Such institutions may

lead to internalized norms so that metaphorical brothers really do excite the same emotional attachment as real brothers. Kinship is a problem for larger-scale institutions, however. In many places, a person who does not funnel the benefits of a leadership position to his relatives would be considered a bad person. Also many criminal organizations are based on extended and fictive kinship. Kinship is a hindrance for large-scale cooperation unless norms sufficiently regulate nepotism to avoid ‘corruption.’

- 2) **Reciprocity:** Children can perform tit-for-tat style reciprocity by age four (Fiske 1991), long before they cooperate or behave fairly with anonymous others (Harbaugh et al. 2002). Reciprocity can sustain cooperation in small groups (less than ten), so organizations should partition units into small groups, to exploit our reciprocity psychology (Boyd and Richerson 1988; Richerson and Boyd 1999). As with kinship, unregulated reciprocity can often undermine larger scale organizations, as when we legislate against cartels so as to force businesses to compete.
- 3) **Negative Reciprocity:** People have a taste for vengeance; if someone hurts them or their kin, they are inclined to strike back. Human communities have to suppress this tendency in order to avoid cycles of vengeance. However, negative reciprocity can be harnessed as a source of motivation to punish norm violators, as long as only norm violator can be punished. Similarly, if norm violator is seen to affect the fate of the entire group, violations can be taken as direct attack on the group (e.g., adultery angers a god; the god may cause a hurricane to strike the village; ergo, my house was destroyed because you committed adultery).
- 4) **Reputation and Signaling:** Humans are concerned both with what our fellows think of us (as potential partner and collaborator) and about whether they consider us moral, or at least good citizens (i.e., internalizers of local norms). If policing or monitoring can be seen as a means of (a) demonstrating one’s talents, or (b) as demonstrating one’s commitment to the group norms, then institutions can sustained by harness this aspect of our evolved psychology (Henrich and Henrich 2007; Bliege Bird et al. 2001).
- 5) **Leadership and Status:** Humans have at least two types of status: dominance and prestige (Henrich and Gil-White 2001; Johnson et al. 2007). Dominance status arises from control over costs and benefits,

and is homologous with dominance in non-human primates. Prestige arises as learners seek out learning opportunities from more successful and competent individuals or because individuals recognize and appreciate other extraordinary contributions to collective welfare. Prestige and dominance are separately underpinned by different suites of emotions, include two different forms of pride (Cheng et al. 2010). Since prestige-related processes favor both altruism and give rise to true influence and persuasion, prestigious leaders can both galvanize more cooperation and potentially spread new norms (Cheng et al. 2011). Since leadership is built on status, social scientists (including anthropologists working in the simple societies) have long observed that there are two kinds leaders (Krackle 1978).

- 6) **Norm Acquisition and Internalization:** Humans are born norm learners (Chudek and Henrich 2010). Young children behave as if they assume that world is full of social rules that they need to learn by observation, and they spontaneously assume others ought to be obeying the norms (Rakoczy et al. 2008). Adults have a keen memory for normative information (O'Gorman et al. 2008). Since learners are unconsciously looking for cues related to emotional reactions, punishment, and conformity to figure out the local rules, these may be useful in spreading novel norms. Relatedly, humans also have to culturally learn what is in a good reputation. Societies vary dramatically in what constitutes a good reputation, or what action cause one to fall into bad standing. Shifting the reputation system (e.g., via the perception that second hand smoke hurts others) can be the fastest way to shift to a new equilibrium.
- 7) **Group Psychology:** Humans seem to have psychological mechanisms for thinking about culturally marked social groupings; ethnic groups are a classic example (Boyd and Richerson 1987; Haslam 2001). The cognitive system has numerous effects but here are three important ones: (1) people tend to essentialize membership in marked groups and readily extend behavioral observations from one member to all (Diesendruck and Gelman 1999; Gil-White 2001), (2) people preferentially imitate in-group members, and (3) people preferentially interact with co-members of salient groups (Kinzler et al. 2007). Our group oriented psychology can be tapped using symbol markers, especially those that are difficult to fake (Henrich and Henrich 2007: Chapter 9). Thus, persuasion by in-group members is often effective, but attempts by out-group members to persuade in-

group members are often remarkably ineffective. Thus, rhetoric and advertisements very often attempt to manipulate identity in order to persuade.

One practical avenue recommended by this approach is not to attempt to design a master solution with forethought, but to, within a population, try different things in different interacting subpopulations. As different subpopulation succeed or fail, less successful groups will imitate the more successful groups creating new recombinations. Over time, as long as the group remains competitive and well-informed of each other's success, competition plus imitation should ratchet up the quality of institutional forms for collective action.

Conclusions

At the beginning of this paper we posed four questions about human cooperation and promised answers. We conclude by returning to those questions.

Why is the scale and intensity of human cooperation (and conflict) so different from other species?

Humans have been subject to a process of gene-culture coevolution. Cultural variation is more strongly affected by group selection than genes, allowing humans to solve dilemmas of collective action on a larger scale than other species. In primitive societies governed by rudimentary norms and institutions, individuals whose genes attracted punishment and ostracism would have been selected against. The resulting population was one in which most individuals readily learn the norms that support institutions and act in accord with them. The capacity to learn norms and operate institutions seems to be fully developed in all ethnographically known societies and was probably in place by 50,000 years ago, if not earlier. Thus today human populations are routinely able to solve problems posed by cooperation and conflict by building systems of norms and institutions. The tribal social instincts in turn act as a moral hidden hand that shapes and selects proximal mechanisms for enforcing norms like punishment and reputation so that institutions are often socially efficient.

Why does the scale vary so much among human societies, with some societies lacking much collective actions beyond the extended family while others organize millions in modern nation-states?

People began to domesticate plants and animals only about 11,000 years ago. Agriculture and the many arts that grew up with it created the potential for

dense societies in favorable locations. Hence villages, towns, and cities began to grow. The pace of evolution varied from region to region, probably for many reasons (Richerson and Boyd 2001), even in the most favorable areas. Today, the world is a mosaic caused by differences in history and ecology. Tropical forest cultivators living a low density in family hamlets have virtually no institutions that operate outside the extended family (Johnson 2003). Densely populated urban cores of societies rich in agricultural, industrial, and human capital resources support modern nation-states. In some places with intermediate productivity or a historically slow trajectory of development tribal-scale institutions are still very strong. Sub-Saharan Africa and parts of the Middle East, most notably the Pashtun parts of Pakistan and Afghanistan are examples (see Turchin's article in this Special Issue). It is important to note that the time scales of cultural change ranges from generations to millennia. If an institution is destabilized it may change rapidly until a new, usually nearby, equilibrium is established. Unless destabilized, institutions are very resistant to change. Policy makers are fated to be frustrated by the slow and hard-to-control nature of cultural evolution.

Why are the solutions to the dilemmas of cooperation reached by different societies so diverse?

In recent years, theorists have discovered many mechanisms that can stabilize cooperation (Chudek, Zhao, and Henrich forthcoming). Various forms of punishment, ostracism of non-cooperators, assortative formation of groups with like propensities to cooperate, cooperation provided as a costly signal in a mating game, and other situations in which payoffs in one game are linked to another by reputations are among the plausible mechanisms that have been studied. Some of these mechanisms are examples of the many equilibria that can be stabilized in repeated games under the Folk Theorem. Others will stabilize an institution even in a non-repeated game. Aoki (2001) and Greif (2006) picture the institution as the self-reinforcing equilibrium of a social game. In the event that a stable equilibrium is perturbed—ongoing internal and external changes will eventually destabilize every equilibrium—the society in question will conduct a local search strategy space for a new equilibrium. Related or sometimes even unrelated societies may provide the inspiration for new norms that stabilize a new equilibrium. Given that many societies comprise many more-or-less linked institutions, the space of all possible equilibria is probably huge. Some will fail and go extinct. Not unlike languages and species that evolve in a very large design space, the evolution of norms and institutions is an inherently diversifying process.

Why do societies sometimes possess norms/institutions that are maladaptive and costly to individuals and groups?

Some of the forces that guide social evolution favor group-functional norms and institutions. We have spoken of cultural group selection and the prosocial biases animated by the moral hidden hand. By these means we hope to explain the gradual increase in the scale of institutions over the last few millennia. Increases in scale of institutions expand the scope for collective action, generally a good thing. However, Dr. Pangloss never got to perfect any of the mechanisms we have discussed. Punishment and similar forms of reinforcement for conforming to a norm can stabilize maladaptive behavior. Outmoded institutions stabilized by pluralistic ignorance are one example. As long as groups have the potential to compete violently, increasing the scale of cooperation can lead to disastrous consequences, as in the nationalistic conflicts of the twentieth Century. The institutions of nationalism seem quite stable in many modern states. Institutions of social dominance in which one group is largely able to dictate to another is perhaps not a good equilibrium even for the dominant class, since enforcement costs are likely to be high. A society may be deeply trapped at an equilibrium that is manifestly sub-optimal compared to other societies yet a set of interlocking institutions may be so complex as to make it difficult or impossible to discover a path to a better equilibrium.

Nothing about norms and institutions makes sense except in the light of evolution. Policy analysts should think of themselves as applied evolutionary scientists for policy making is a form of artificial selection aimed at deliberately changing the norms and institutions of a society.

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